

THE CRANIAL MORPHOLOGY OF
THRINAXODON LIORHINUS SEELEY

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(With 33 figures)

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INTRODUCTION

When Owen introduced the term 'Cynodontia' in 1861, he made *Galesaurus*, which has a mammal-like dentition, the type of the new group which he called a 'family' of the order Anomodontia. Only in 1876 did he create the order Theriodontia to receive all forms with a carnivorous mammal-like dentition. *Lycosaurus*, *Nyctosaurus* and *Scaloposaurus* were included in this order. The former, which was the type of the order, has simple, pointed teeth whereas the two other genera have laterally cuspidate postcanines. Obviously the Theriodontia were therefore meant by Owen to include more than his Cynodontia.

Because the crowns of the postcanines were not preserved in the *Galesaurus* specimen originally used by Owen (1861) as the type of his Cynodontia, Seeley (1895b: 59) proposed that the name Cynodontia be used for animals which resemble *Galesaurus* in skull structure and *Nyctosaurus* in the structure of the postcanines, because it was possible to distinguish the Cynodontia from the Lycosauria (Theriodontia) ' . . . by dental and other minor characters of the skull'. Seeley therefore designated *Cynognathus*, which he described in that year, as the type of the more narrowly defined Cynodontia. In 1903 Broom pointed out that the Theriodontia was not a natural order and proposed that it be broken down into Cynodontia and Therocephalia. Among these Cynodontia none is better known today than *Thrinaxodon*.

The first skull of *Thrinaxodon* was described by Owen in 1887, but he referred it to *Galesaurus planiceps*. In this identification he was followed by Seeley (1889) and Lydekker (1890). Only in 1895, on comparing the postcanine crown patterns of *Galesaurus planiceps* and *Nyctosaurus larvatus* did Seeley

(1895a) realize that the skull belonged to a new genus and species for which he proposed the name *Thrinaxodon liorhinus*. Van Hoepen (1916), Gregory (1920) and Haughton (1920, 1924), when describing specimens now recognized as members of the genus *Thrinaxodon*, referred them to *Ictidopsis*, a name introduced by Broom in error in 1912. Since these two names refer to identical forms, the term *Thrinaxodon*, introduced by Seeley in 1894, has preference.

In 1932 Broom added the species *T. putterilli* to Seeley's original *T. liorhinus*. *Thrinaxodon* has become the best known of the Galesauridae and Cynodontia as a result of the studies of Broom published in several papers between 1910 and 1938, Watson (1920), Parrington (1933, 1935, 1936, 1939, 1946), Olson (1944), and Brink (1954, 1955b). More recently Estes (1961) elucidated the cranial structure of *Thrinaxodon* with emphasis on young individuals. Crompton (1963a) and Osborn & Crompton (1973) explained tooth replacement in *Thrinaxodon* and its significance in relation to mammalian evolution. Crompton & Jenkins (1968) demonstrated the importance of the dentition of *Thrinaxodon* in the evolution of molar teeth and the development of molar occlusion in the first mammals of the late Triassic. Hopson (1966), in a discussion of the origin of the mammalian middle ear, described the condition in *Thrinaxodon* and noted that the functional aspects of the cynodont middle ear are not understood well enough to say much about acuteness of hearing, but the largeness of the fenestra ovalis relative to the apparent size of the tympanum, which had an area of one-ninth or less of that of the former, would probably have made the sensitivity to sound much lower than in living reptiles.

Van Heerden (1972) has just completed a revision of some of the Galesauridae. He demonstrated the identity of *Thrinaxodon putterilli* with *Thrinaxodon liorhinus*. The type specimens of *Notictosaurus luckhoffii* and *N. gracilis*, declared identical with each other by Brink (1965), have now been shown to be identical with *T. liorhinus*. Van Heerden's investigations have greatly extended the territorial distribution of *Thrinaxodon* between Harrismith and vicinity in the north-eastern Orange Free State and Thaba N'chu more west and south, much further south to the vicinity of the Hendrik Verwoerd Dam near Bethulie, then on to the vicinity of Burgersdorp slightly more south-east and to Graaff-Reinet in the far south-west. Finally the value of the detailed description by Jenkins (1971) of the postcranial anatomy of *Thrinaxodon* and other African cynodonts should be mentioned in this brief survey of important contributions to our knowledge of *Thrinaxodon*.

In 1938 Broom had a skull sectioned at intervals of 4 to 5 mm. Considerable detail of internal structure and some of tooth replacement was obtained. The intervals between sections were, however, large and much detail was lost. Consequently accurate interpretations were difficult and several minor errors slipped in. Broom himself realized the inadequacy and suggested that a much larger series of sections and photographs be made in order '... to clear up all the characters of the prootic and opisthotic and to reveal the structure of the labyrinth'. Some of this additional information was obtained by Olson (1944)

when he sectioned a skull at intervals of 0,37 mm. He concentrated on the braincase, otic region and base of the skull.

Parrington's paper of 1946 added much new information, but it was felt that serial grinding at closer intervals than those taken in previous investigations might settle doubtful points, and reveal additional information especially on tooth replacement, the course of some of the nerves and blood vessels, the middle and inner ear, the relationships of the elements forming the braincase, the relationships of the postdentary bones, and the origins and insertions of jaw muscles and correlated skull structure. With this purpose in mind the study on which the present paper is based was started.

The skull of *Thrinaxodon liorhinus* Seeley selected for sectioning measured 67 mm from the tip of the snout to the posterior termination of the parietal crest. It was catalogued as number C354 of the National Museum, Bloemfontein, and was very well preserved, showing hardly any distortion. The snout was slightly damaged and the right postorbital arch was incomplete. Several detached pieces of bone lodged in the matrix were possibly derived from the broken regions. Serial grinding was done at intervals of 0,2 mm. Enlarged drawings were used for making graphic reconstructions and for building a wax plate model (5 ×, linear) of the skull. Crompton's (1955a) modified method based on the original technique described by Sollas (1914) and Olson (1944) was used. Photographs were taken of sections featuring important detail.

Before the completion of the original work on which this paper is based, the paper by Estes (1961) appeared which shed further light, especially on growth changes in the *Thrinaxodon* skull.

Through these studies the taxonomic position and external features of the skull and skeleton of *Thrinaxodon* have become well known. During the last five years it has become more and more evident that *Thrinaxodon* was an animal of crucial importance in the evolution of the first mammals.

In his discussion of the lower jaw of cynodonts and the evolutionary origin of the mammal-like adductor jaw musculature Barghusen (1968) showed that in *Thrinaxodon* a muscle mass with relationships approaching those of the mammalian masseter muscle had developed. The development of this musculature is intimately related to and can account for the relative posterior expansion of the ventral portion of the dentary ramus. This extra surface was included by the masseter muscle. Contrary to Crompton's (1963b) view, Barghusen shows that the adductor musculature did not migrate from the reflected lamina on to the ventral part of the masseteric fossa, but that the external adductor muscle (Crompton's deep masseter) on the dorsal lateral part of the dentary in procyonuchids migrated downwards (ventrally) and at the same time the entire length of the zygomatic arch was established as an area of muscular origin. The cynodont masseter is therefore a new differentiation not found in other therapsids.

The second change in cynodonts was the development of a pattern of insertion characteristic of the mammalian temporalis muscle. This was accomplished

through the posterodorsal expansion of the coronoid process of the dentary. As a result of these modifications cynodonts established an arrangement of adductor jaw musculature closely approaching that in living mammals. Crompton (1963*b*) had shown that in a stratigraphic series of cynodont lower jaws progressive osteological changes not found in any other group of reptiles took place. These changes were the progressive enlargement of the posterior part of the dentary and concomitantly the reorientation in position and reduction in size of the accessory jawbones. Both Crompton and Barghusen relate the osteological changes in the lower jaw to the development of the mammalian type jaw musculature. Thus differentiation of jaw musculature in early cynodont evolution (procynosuchids to *Thrinaxodon*) is the key innovation that had profound significance for the origin of mammals.

In 1967 Hopson, in a discussion of mammal-like reptiles and the origin of mammals, concluded that early mammals could all be derived from small, probably insect-eating early Triassic cynodonts with skull and dental characters like those of *Thrinaxodon*. Some indication of the possible continued existence in the late Triassic of persistently small, dentally conservative cynodonts which were acquiring mammalian features in parallel with their larger more specialized relatives is a single poorly preserved skull of a very small cynodont with *Thrinaxodon*-like teeth from the Middle Triassic.

On the basis of the fact that the crown structure of one of the generations of postcanine teeth of *Thrinaxodon* is almost identical to that of *Eozostrodon*, except that the *Thrinaxodon* postcanines have a single root, and due to the overall primitive structure of the primitive cynodont skull, Crompton & Jenkins (1968) concluded that Rhaetic mammals (excluding ictidosaurids and haramyids) could be derived from primitive cynodonts. They point out that new material shows that it is possible to derive the cynodont petrosal and alisphenoid from that of a scaloposaurid, and that the eozostrodonid petrosal, as it is known at present, can be derived from that of an early cynodont of which the anterior margin is more complex than is shown in published accounts.

The view that mammals can be derived from persisting members of the cynodont family Galesauridae, of which *Thrinaxodon* is the most important known member, is reiterated by Hopson & Crompton (1969). They state that only cynodonts possess a large suite of features elsewhere found only in mammals. They believe that mammals had a monophyletic origin at the low taxonomic level of a family or even lower.

At present active research is being conducted on late cynodonts of East Africa and South America, in which information on the transitional stages between the early South African cynodonts and the first mammals is sought. In spite of all past and recent work, problems of functional anatomy and evolutionary transformation still remain. It is hoped that the results described in the present paper might, though obtained about ten years ago as part of the work for a doctoral thesis, still be able to contribute to the detailed comparison of structure in early and later cynodont and early mammalian skulls.

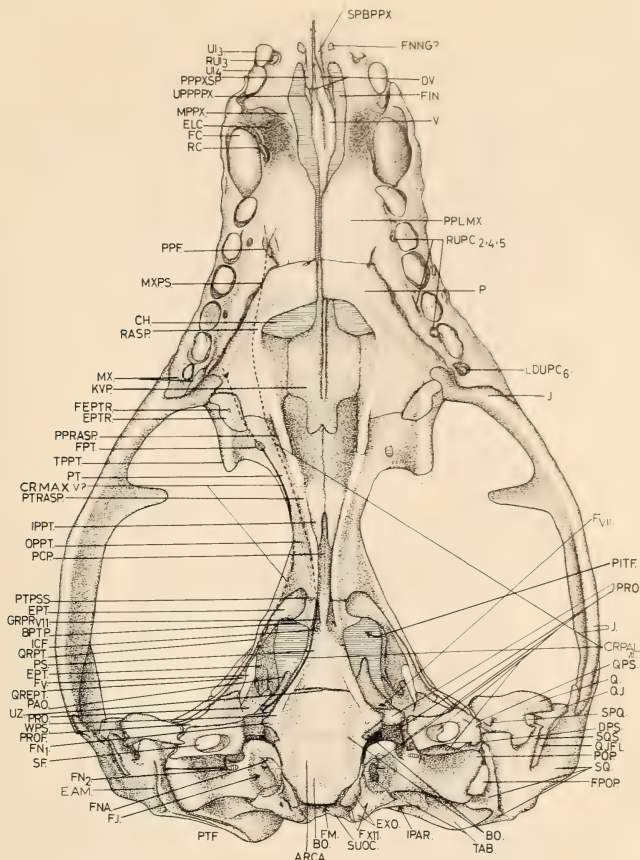


Fig. 1. Graphic reconstruction of ventral view of serially sectioned skull shown as a mirror image. $\times 1.5$.

DESCRIPTION OF MATERIAL

(a) SKULL (Figs 1, 2)

In this section only new details that have appeared from the present study will be mentioned.

Premaxillary (Figs 1, 3-6)

Behind the first incisor in each premaxillary is the small foramen (Figs 1, 33C, FNNG) of a vertical canal which may have had some connection with an organ of Jacobson or a nasal gland connected with the ability to detect odours. The canal appears to have a horizontal branch which opens on the anterior surface of the premaxillary immediately below the base of the internarial process. The vertical canal apparently opens on the floor

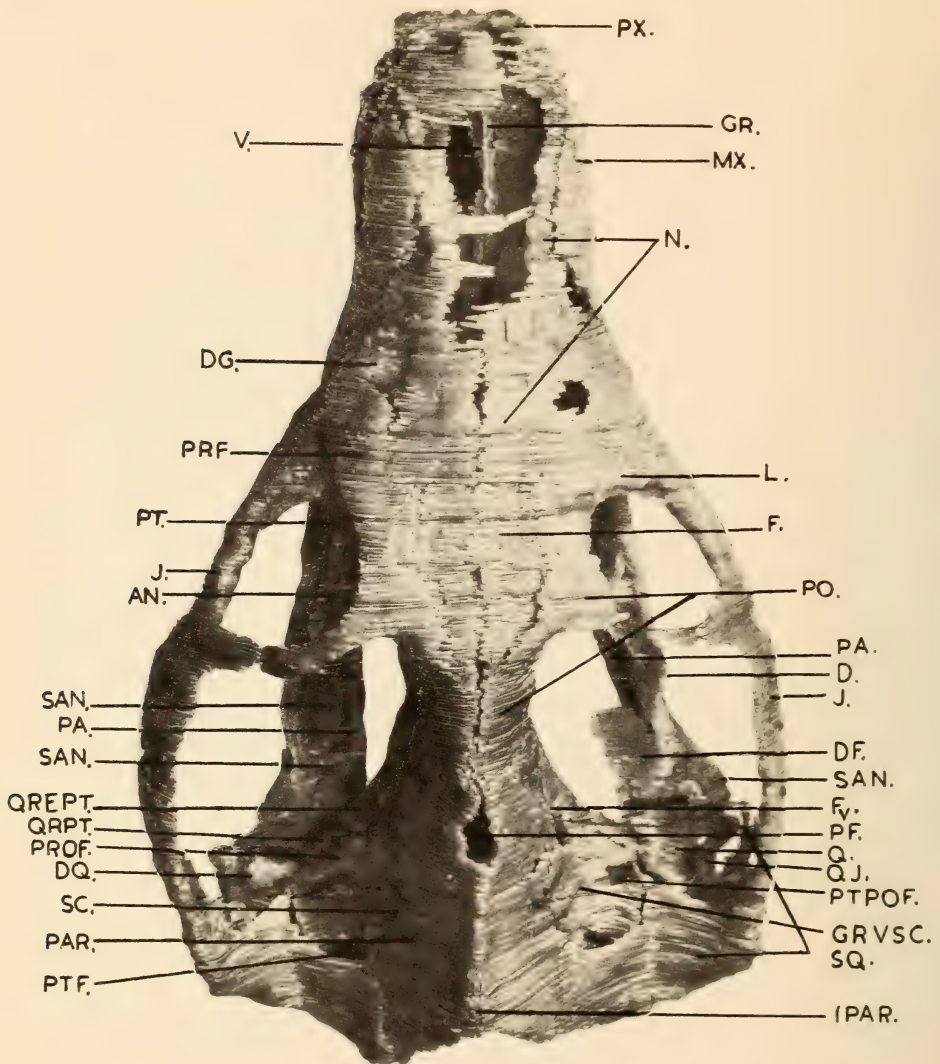


Fig. 2. Dorsal view of model of serially sectioned skull of *Thrinaxodon liorhinus* built on a linear magnification basis of $\times 5$. Roof of snout damaged. Photograph shows model reduced to $\times 2$ original size of skull.

of the nostril just behind the internarial process. It appears to be very similar to the canal described by Brink (1961*b*). Similar canals are present in the higher cynodonts as well as in primitive forms like the scalposaurids.

In medial view, the palatal process of the premaxillary is bifid. The upper prong (Figs 1, 3A, 4B, 5, UPPPPX) is long and extends backward as far as the canines (Figs 1, 3A). The shorter lower prong (PPPXSP) in dorsal

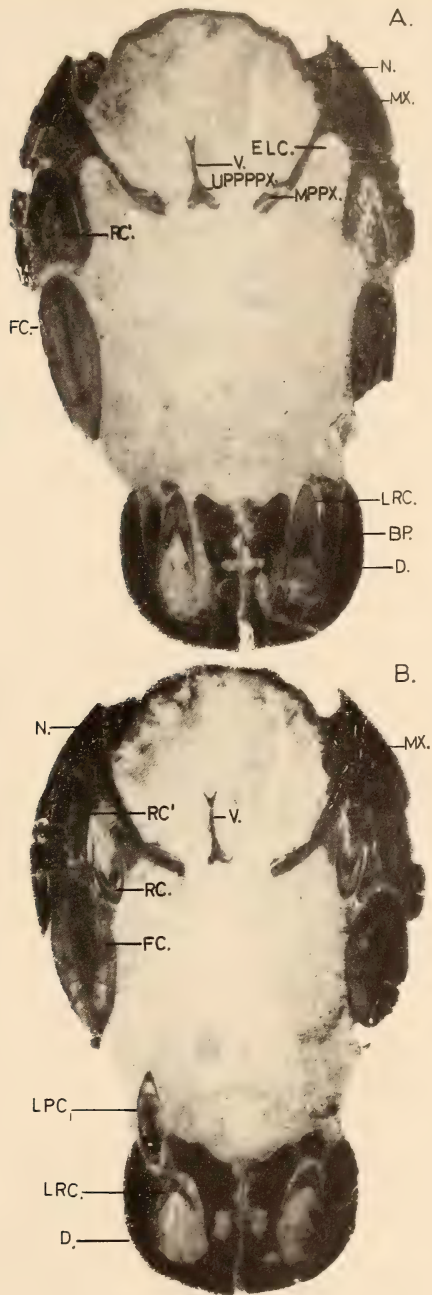


Fig. 3. A. Transverse section showing relationship of vomer, premaxillary and maxillary, and replaced upper canine; B. Transverse section showing replacing canine. Both $\times 3$.

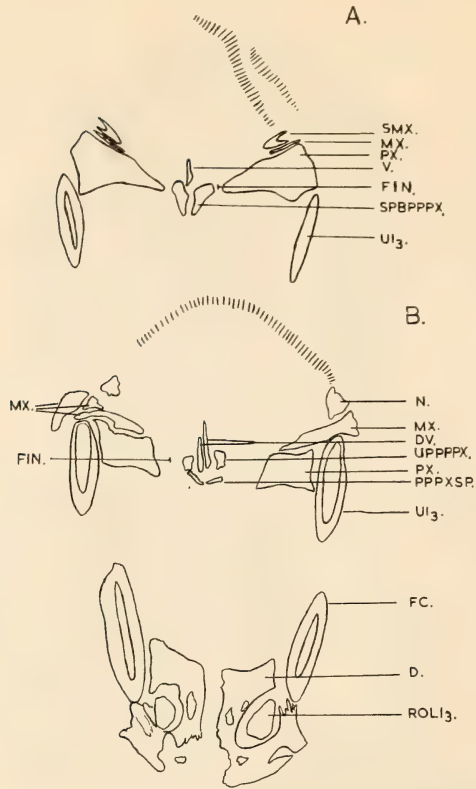


Fig. 4. Transverse sections through snout. A. Septomaxillary and palatal process of premaxillary. B. Double anterior end of vomer and palatal process of premaxillary. $\times 3$.

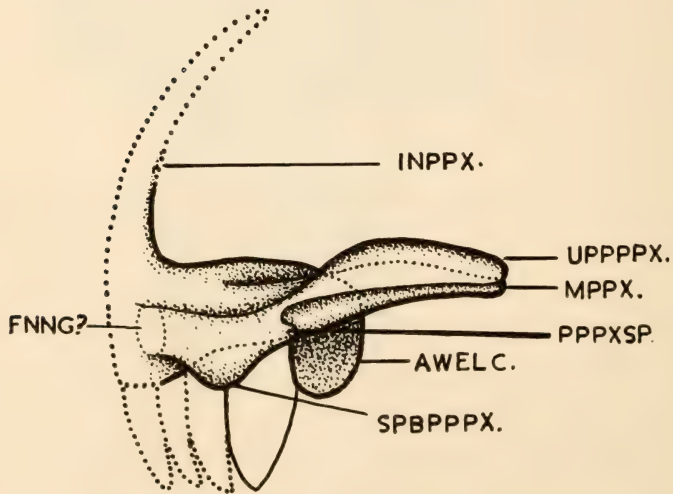


Fig. 5. Graphic reconstruction of medial view of premaxillary. $\times 5$.

view is partly hidden by the upper prong (Fig. 4B). In palatal view (Fig. 1), however, it largely obscures the upper (dorsal) prong. Ventrally at the base of the palatal process is a very small process (Figs 1, 4A, 5, SPBPPPX) situated on a low ridge along the medial ventral margin of the palatal process. A similar process is present in the cynognathids and *Diademodon* (Brink 1955a).

The lateral part of the premaxillary (i.e. palatal process excluded) forms the anterior wall of the pit for the lower canine. The premaxillary extends backwards medially alongside the ventral edge of the pit. This extension of the premaxillary (MPPX), referred to as the maxillary process of the premaxillary, is held in a groove along that part of the maxillary which forms the medial wall of this pit for the lower canine (Fig. 3A). A similar relationship is found in *Diademodon* and the cynognathids.

The anterior palatal foramen or foramen incisivum (Figs 1, 4A, B, FIN) is enclosed between the maxillary and palatal processes of the premaxillary. The ventral surface of the anterior part of the vomer (V) is clasped between the two palatal processes of the premaxillaries (Figs 1, 4A, B).

Maxillary (Figs 1–14A)

Most of the secondary palate is formed by the maxillary. The posterior palatal foramen (Figs 1, 9A, PPF) is about 2 mm long. It is situated on the suture between the maxillary and the palatine, but is largely formed by the maxillary. On the side wall of the snout the dorsal region of the maxillary (MX) lies lateral to the nasal (Figs 2, 3, 6B) and its posterior region overlaps the lacrimal (Figs 2, 6B, 9B, L).

It is interesting to note that many foramina (see e.g. Figs 8A, B, RHC), both large and small, perforate the anterior regions of the dentary, premaxillary and maxillary. The canals from these foramina join a single large canal in each side wall of the snout and in each ramus of the lower jaw. This fact lends support to the suggestion originally made by Watson (1931) when discussing the maxillary of the bauriamorph *Ericiolacerta parva*. He stated (p. 1168): 'This surface is perforated by many foramina. . . . These foramina must have transmitted the blood-vessels and nerves to the skin of the face, their size suggesting that the nerves were exceptionally big, a condition only to be explained by the existence of a series of important tactile sense-organs grouped around the end of the muzzle, that is of what in a mammal would be a rhinarium.' However, Estes (1961) has shown that the vascularization of the *Thrinaxodon* snout does not necessarily indicate a rhinarium, since Van Valen (1960) has described similar vascularization in living reptiles such as *Tupinambis*. Estes claimed that the numerous foramina actually preclude the presence of a movable muscular cheek and lip.

Unfortunately, preservation of the anterior part of the maxillary is not perfect. There appears to be little doubt, however, that a big foramen is situated on the anterior part of the maxillary which forms the wall of the pit for the lower canine. (Estes (1961, pl. 2, fig. 1) actually shows a large foramen in this position.)

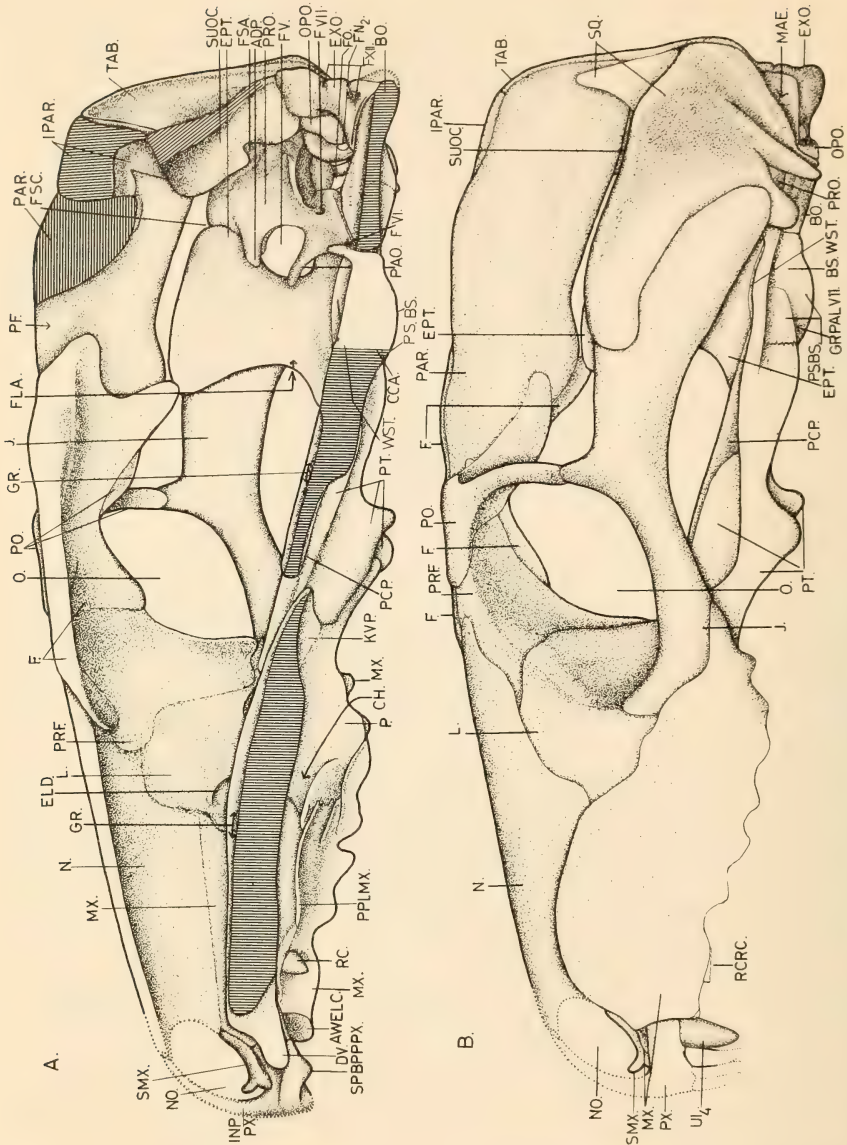


Fig. 6. Graphic reconstructions of serially sectioned skull. A. Median-sagittal view. Hatched surfaces indicate structures sectioned in median-sagittal plane. B. Lateral view; quadrate and quadratojugal removed. $\times 2$.

This foramen may be the anterior end of the canal probably for the main branch of the maxillary nerve (see e.g. Figs 9, 10, CMN) which receives many smaller branches from other parts of the snout.

In sections it appears as if the canal runs back into the base of the canine alveolus, behind which it re-emerges as a distinct canal in which it is assumed the maxillary ramus of the trigeminal nerve and blood-vessels ran (Fig. 10, CMN). Immediately behind the canine alveolus several canals open on to the

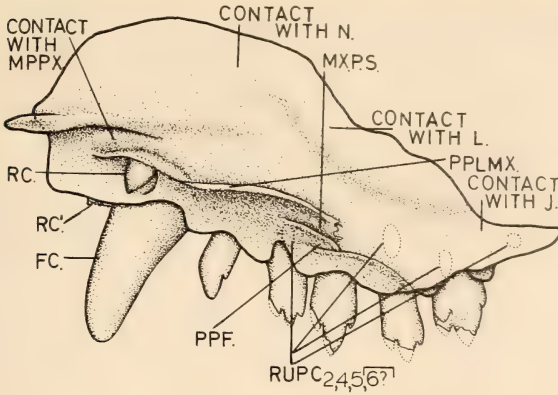


Fig. 7. Graphic reconstruction of maxillary in medial view.
 × 2,5.

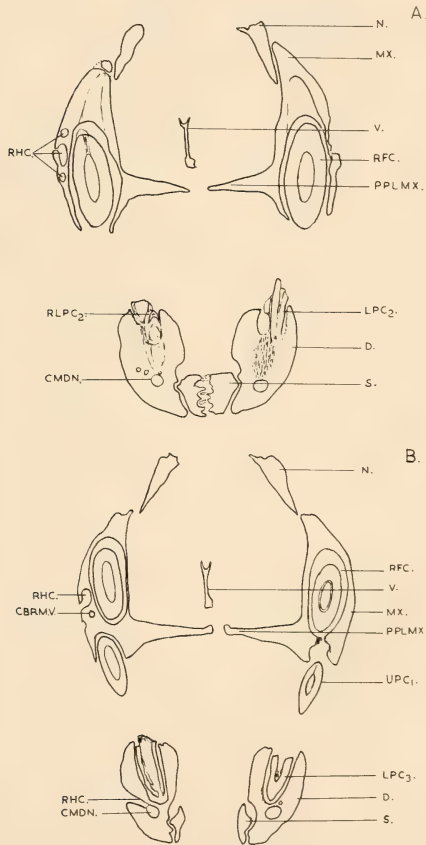


Fig. 8. Transverse sections through snout and lower jaw showing root of functional upper canine, foramina and canals in maxillary and dentary. Note splenial part of lower jaw symphysis in A. × 2,25.

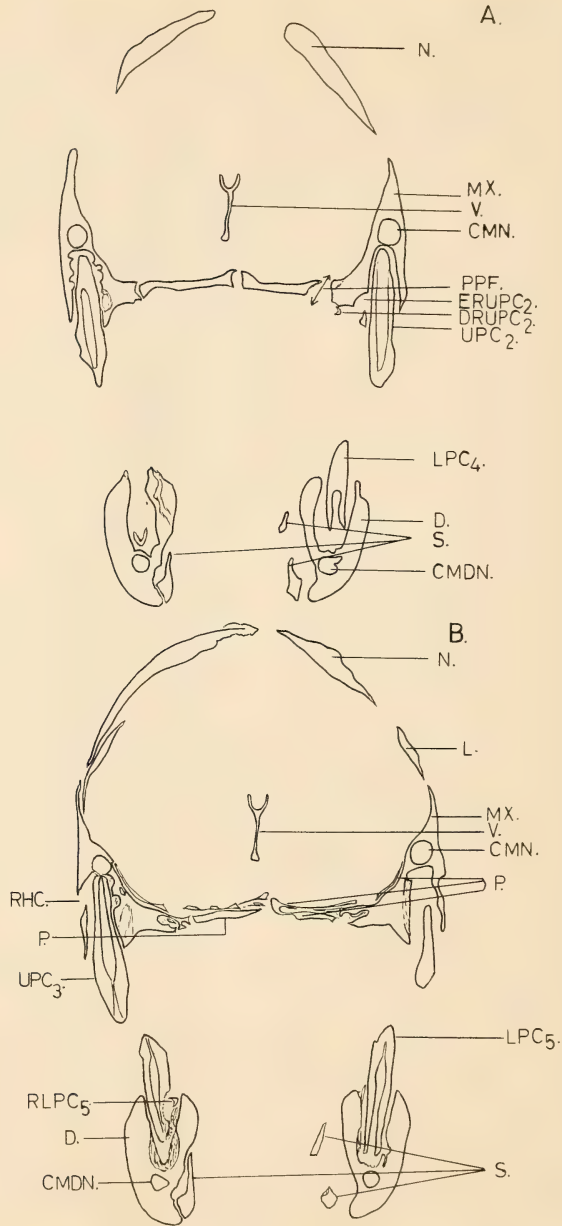


Fig. 9. Transverse sections through snout. A. Posterior palatal foramen; B. Maxillary-palatine suture in this region. $\times 2,5$.

outer surface of the maxillary. These canals join the maxillary canal which runs backwards in the bone. A small canal joins the base of the first postcanine alveolus with the maxillary canal running above it (Fig. 10). Further back the maxillary canal makes direct contact with the bases of the second and third postcanine alveoli. Several more little canals penetrate the maxillary walls of the postcanine alveoli and open into the alveoli. From here the nerves and/or blood-vessels in the canals may have been joined to the nerve and blood-vessels in the maxillary canal. After entering into the base of the third alveolus the main

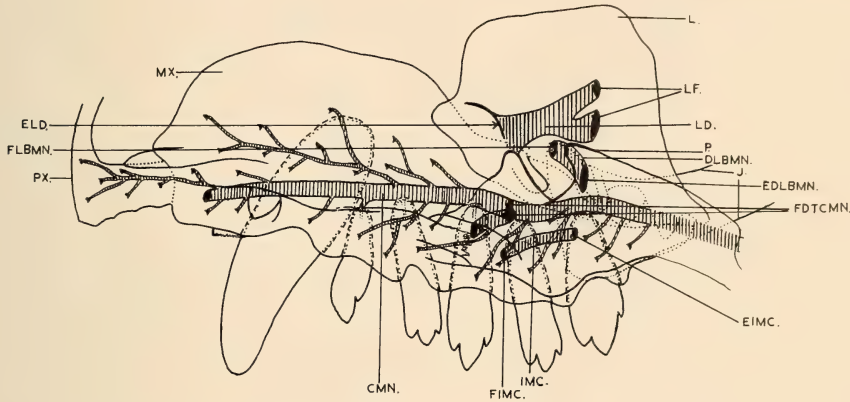


Fig. 10. Graphic reconstruction of canal system in wall of snout. $\times 2.5$.

maxillary canal is joined by a second one, the external opening of which is in the alveolar wall of the third postcanine (Figs 10, 13B, (F)DTCMN). These two canals enter (Fig. 13B₃, FDTCMN) into the 'maxillary antrum' (Fig. 13B₃, MAN) above the fourth postcanine alveolus and at a level just behind the transverse part of the maxillary-palatine suture. The foramen for this second branch of the ramus maxillaris of the trigeminal is also shown by Estes (1961, pl. 2, fig. 1). Kühne (1956, figs 4a, 5a) found that in *Oligokyphus* the ramus maxillaris also splits into two branches.

The maxillary antrum is formed in mammals by the maxillary only. In *Thrinaxodon* the posterior part of the maxillary has a considerable overlap with the lower part of the lacrimal laterally (see Figs 6, 10, MX, L) to form the outer wall of a cavity (Figs 11A, 13B₃, MAN). The floor of this cavity is formed by the maxillary, and its medial wall is formed by a dorso-laterally extending lamina of the palatine (Figs 12, 13B₃, P). This palatine lamina overlaps the lower part of the lacrimal, which forms the roof of the cavity, medially. The 'maxillary antrum' thus formed extends back as far as the sixth postcanine. Its medial wall is not complete, being interrupted behind the palatine lamina where the antrum is only a high, but shallow recess below the anterior part of the lacrimal. The palatine and lacrimal are then reunited in a serrated suture to form a solid

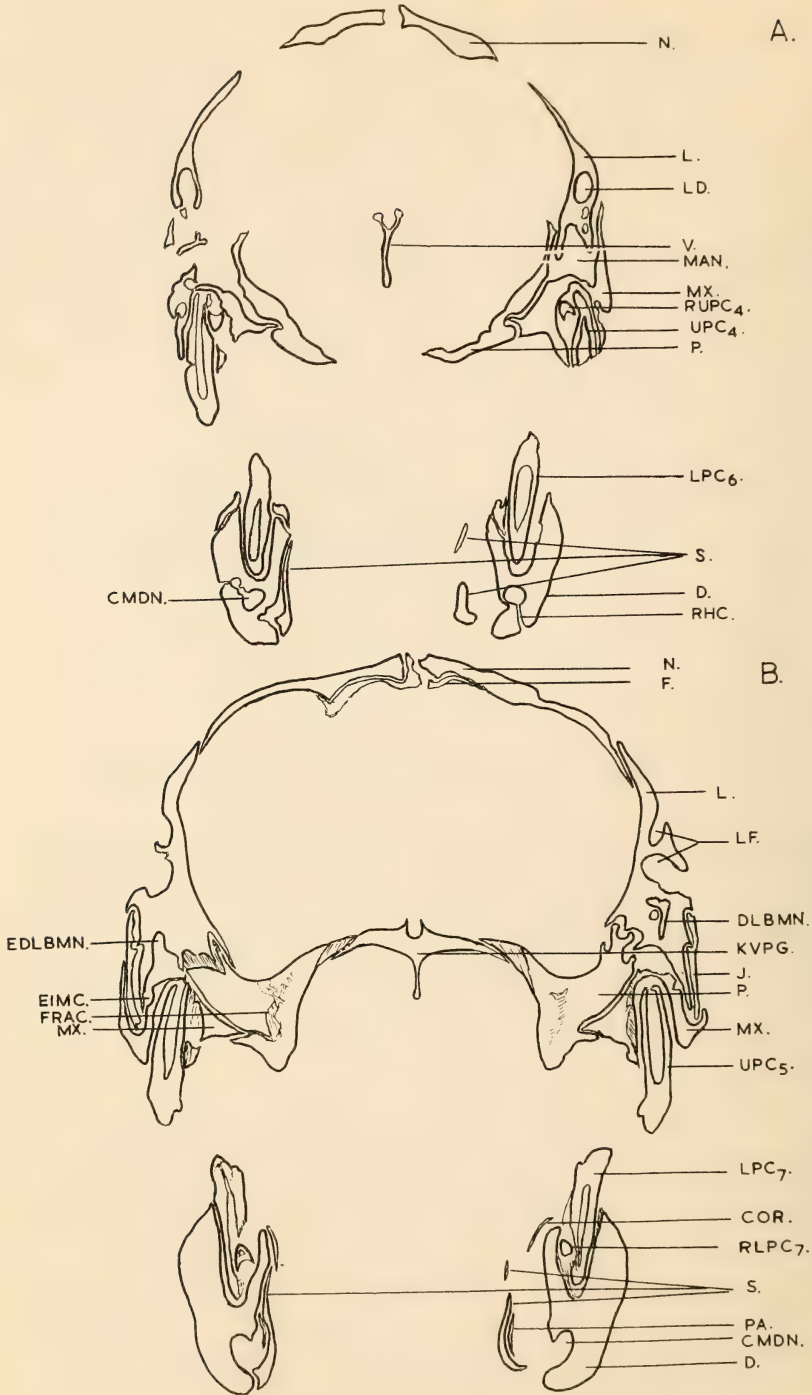


Fig. 11. Transverse sections through snout in the region of: A. Choanae and maxillary antrum; B. Roof of nasopharyngeal passage and lacrimal foramina. Note: relationships of maxillary, palatine, lacrimal and jugal; shape of vomer; structure of lower jaw especially as far as position of mandibular canal is concerned. $\times 3$.

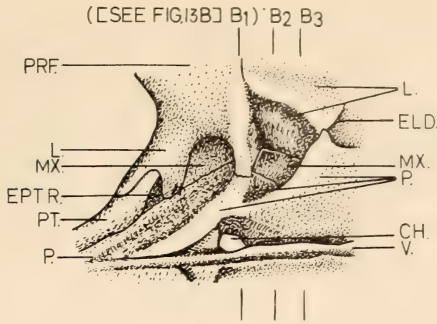


Fig. 12. Medial view of wall of snout of enlarged wax reconstruction of serially sectioned skull to show shapes and relationships of bones along the various parts of the maxillary antrum. $\times 2,5$.

bridge of bone lateral to which the 'maxillary antrum' continues (Figs 11A, 12). At this level the jugal (Fig. 11B, J) takes part in the lateral wall of the antrum. It is held between the lacrimal medially and a lamina of the maxillary laterally. The anterior palatine-lacrimal contact is 1,2 mm and the posterior bridge 1,4 mm in length. Beyond this bridge the antrum continues as a low, but deep recess 2,6 mm long, between the lacrimal and the maxillary (Fig. 12). The recess becomes progressively lower and ends at the level of the posterior margin of the sixth upper postcanine.

In lateral view the foramen of a canal (Figs 10, 13B, IMC), which penetrates the maxillary for 3 mm, is present at the level of the anterior border of the fourth upper postcanine and the 'maxillary antrum'. This canal opens posteriorly into the 'maxillary antrum' at the level of the palatine-lacrimal bridge. Its actual opening (Figs 10, 11B, EIMC) is medially at the base of the lateral lamina of the maxillary and directly below the lateral lower margin of the lacrimal, both of which take part in the formation of the outer wall of the antrum. The significance of the canal described here is uncertain, but it may have been for a third branch of the maxillary ramus of the trigeminal nerve. The latter appears to have swung down from behind the 'maxillary antrum' on to the dorsal surface of the palatine. Here it might possibly have been joined by the ramus palatinus of the facial nerve (Fig. 16A, CRPAL_{vii}) which probably left the palate through the posterior palatal foramen (Figs 1, 16A, B, PPF). Both branches then apparently continued further backwards on the pterygoid. Their further course is discussed below (see Pterygoid, p. 357).

Lacrimal (Figs 2, 6, 10-14A)

The lacrimal forms the anterior wall of the orbit (Fig. 6B). It extends forward as far as the third upper postcanine and the transverse part of the maxillary-palatine suture on the secondary palate. In sections the lacrimal appears mainly

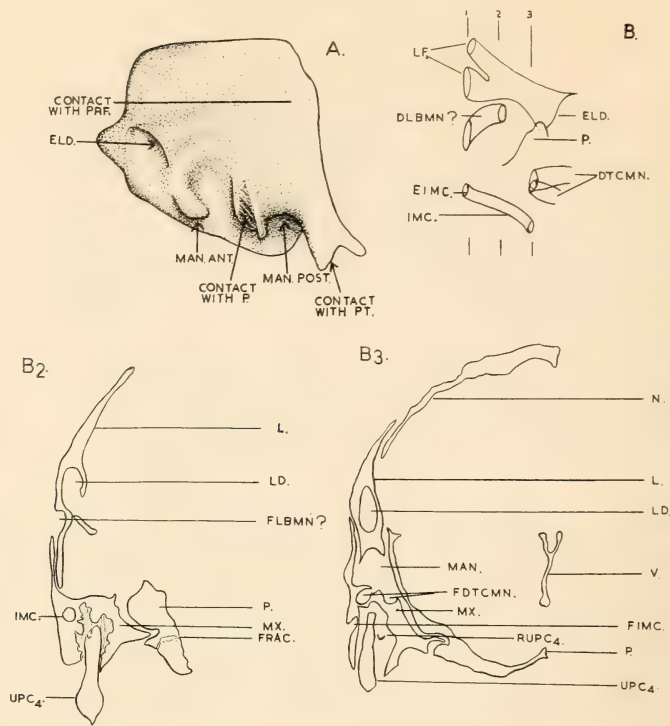


Fig. 13. A. Graphic reconstruction of medial view of lacrimal. B. Canals in wall of snout also shown in Fig. 10. Numbered levels coincide with those shown in Fig. 12. B₂ and B₃ are transverse sections from levels numbered 2 and 3 in B, or B₂ and B₃ in Fig. 12. $\times 2,5$.

as a thin sliver of bone with the exception of a thickened middle part which contains the lacrimal duct. In lateral view the lower part of the bone is overlapped by the posterior part of the maxillary, and the dorsal part of the lacrimal is just overlapped by the ventral margin of the posterior part of the nasal (Fig. 6A, MX, L, N). Unfortunately the preservation of this part of the snout is not as good as could be desired and the sections are difficult to interpret. The lacrimal also overlaps the anterior ventral part of the prefrontal (Fig. 6A, PRF). The anterior opening of the lacrimal duct (Figs 6A, 10, 12, 13A, B, ELD) is near the anterior end of the bone just above and in front of the anterior part of the wall of the 'maxillary antrum'. The maxillary forms a distinct ledge below the opening. In a posterior direction this ledge becomes more pronounced to form the floor of the 'maxillary antrum', but in front of the opening the ledge very gradually becomes indistinct.

Where the palatine and the lacrimal form the bridge which is part of the inner wall of the 'maxillary antrum' described above (see Maxillary), the lower

part of the lacrimal is wider than anywhere else when seen in section (see e.g. Fig. 11B, L). Between the fourth and fifth upper postcanines is the anterior foramen (Figs 10, 13B₂, FLBMN) (Estes (1961, pl. 2, fig 1) also shows this foramen) of a canal (Figs 10, 13B, DLBMN) which runs in the lacrimal just below the lacrimal duct. The lacrimal duct itself divides into a small upper and a larger lower duct only 1 mm behind the level of the foramen just mentioned (Figs 10, 13B) and opens (Figs 10, 11B, 13B, LF) into the orbit only 0.6 mm behind the division. The other canal turns sharply downward (Figs 10, 11B, 13B DLBMN) at this level and enters (Fig. 11B, EDLBMN) into the posterior part of the 'maxillary antrum', the inner wall of which is formed at this level by the palatine-lacrimal 'bridge'. This canal appears to be comparable with the one which Kühne (1956: 28, fig. 5) described in *Oligokyphus* as the canal for the lacrimal branch of the maxillary ramus of the trigeminal nerve.

It seems reasonable to assume, on the basis of the canals described above in the maxillary and lacrimal, that the ramus maxillaris of the trigeminal nerve was made up of the following branches (Fig. 10):

- (a) the main anterior branch made up of smaller branches from the tip of the snout, the incisors, the canine, the first two postcanines and the snout in their vicinity, joined by
- (b) a second branch from the side of the snout in the vicinity of the third postcanine. These two branches (*a* and *b*) entered the 'maxillary antrum', in the posterior part of which they were joined by
- (c) an independent branch of unknown significance, possibly a third branch of the ramus maxillaris, and
- (d) a lacrimal branch.

The compound maxillary ramus then left the 'maxillary antrum' and might have been joined a little further back by the ramus palatinus of the facial nerve.

The wide basal part of the lacrimal just in front of the narrower posterior end of the bone has a somewhat spongy structure which makes it difficult to reconstruct the course of a possible canal in this part of the bone from serial sections. There does, however, appear to be a canal which may then be compared with the vascular canal found by Kühne (1956: 28, fig. 5) in *Oligokyphus*.

Palatine (Figs 1, 6A, 9B, 11A–16B)

The maxillary is continued postero-laterally beyond the posterior palatal foramen, but it is overlapped on its medio-dorsal surface by the palatine (Figs 11A, 12, 13B₂, 13B₃, P, MX). This overlapping dorsal part of the palatine has a very thin upper rim of which the margin is expanded laterally and medially to form a distinct ridge. It is this thin upper end which forms the medial wall of the anterior part of the 'maxillary antrum' (Figs 12, 13B₃, P, MAN), the ridge being in contact with the medial surface of the lacrimal. The palatine and the maxillary are joined by a thin ledge which projects from the medial border of the maxillary into a groove along the lower lateral surface of the palatine (Figs 11,

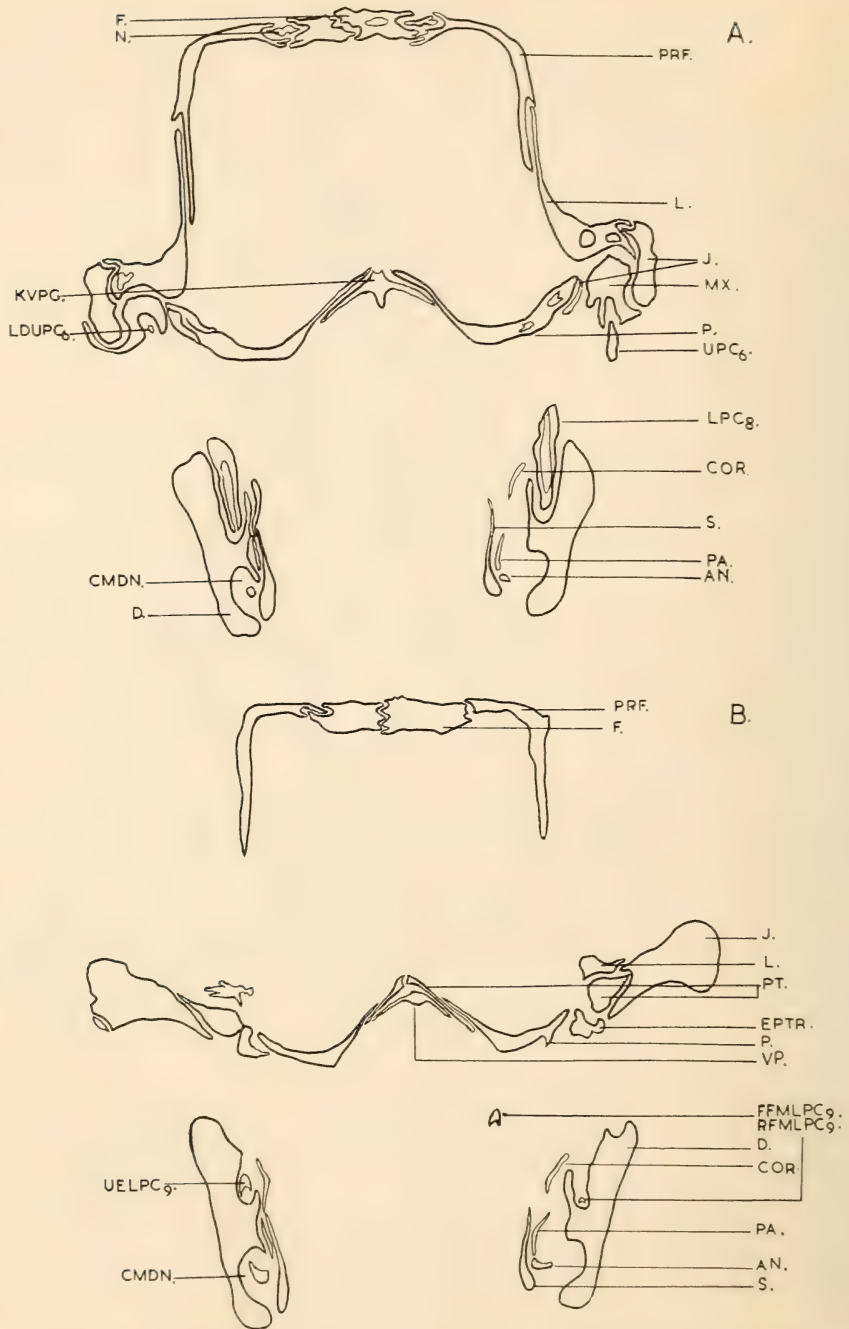


Fig. 14. Transverse sections through skull and lower jaw; A. At level in anterior part of orbit; B. Slightly further back. Note: anterior ends of pterygoids and ectopterygoids in B and of the angulars in A; posterior ends of nasals and maxillaries in A and of the lacrimals in B; extension laterally of jugals. $\times 2,5$.

13B₂, B₃) (a schindylesis or wedge-and-groove suture). The two bones lie close together at all their contact surfaces.

Ectopterygoid (Figs 1, 14A, 15A, 16A)

Parrington (1946) describes two foramina in this bone, but it seems to be a variable feature since the sectioned skull shows only one (Fig. 1, FEPTR). This single foramen is situated almost in the position of Parrington's anterior one, but it lies nearer the inner surface of the ridge.

Vomer (Figs 1, 3, 4, 6A, 8A-9B, 11A-12, 13B₃, 14A-15A)

The vomer has several features of interest. The posterior curved plate-like part forms the roof of the nasopharyngeal passage behind the secondary palate (Figs 1, 11B, 14A, B, (K)VP(G)). Antero-dorsally it is overlapped by the palatines (Figs 1, 4A, P) and postero-dorsally by the pterygoids (Figs 1, 14B, PT). The part comprising the thin median vertical plate extends forward into the lower half of the snout (Figs 1, 6A, 11A, V) to be clasped anteriorly by the upper prongs of the palatal processes of the premaxillaries (Figs 1, 3A, 4B, 6A, UPPPPX). Nowhere is the median vertical plate of the vomer in contact with the maxillaries. The front end of the vertical plate, which extends forward to a level with the fourth incisors, is bilaterally paired for a distance of 3.4 mm (Figs 1, 4B, 6A). A line of fusion can, however, be distinguished much further back. Anteriorly the lower end of each plate curls slightly outwards, but behind the line of fusion and as far back as the posterior border of the lower canine pit they curl pronouncedly (Figs 1, 3A, B). This condition is also found in higher cynodonts investigated by the present author and by Broili & Schröder (1934a). It need not cast doubt on the homology (proposed by Parrington & Westoll 1940) of this structure and the mammalian vomer which usually arises singly, since De Beer (1937: 434) gives examples of a paired origin of the vomer in mammals.

Together with the upper prongs of the palatal processes of the premaxillaries (UPPPPX) which also extend back to the level of the posterior margins of the lower canine pits, the vomer with its curling lower ends forms a rod in which the component parts support each other. This rod, of which the ventral surface is grooved (due to the curling vomer), divides the large foramen, situated ventrally between the premaxillaries, into a left and right foramen incisivum (Figs 1, 4A, B, FIN). The palatal plates of the maxillaries form the posterior border of each foramen. Above the palatal plates of the maxillaries, but not in contact with them, lies the vertical vomer plate of which the ventral margin is, in this region, thickened and rounded (Figs 1, 8A, B, V). The upper margin of this vomer plate has a distinct groove (Figs 3, 6A, GR). The groove extends back over the whole length of the vomer (Figs 3, 6A-11B, 14A), presumably over the pterygoids (where it may, however, be interrupted) and on to the rostrum of the parasphenoid (Figs 6A, 15C, 16A, 17, PCP). A similar condition is found in the cynognathids and in *Diademodon* (Brink 1955a). This groove probably supported

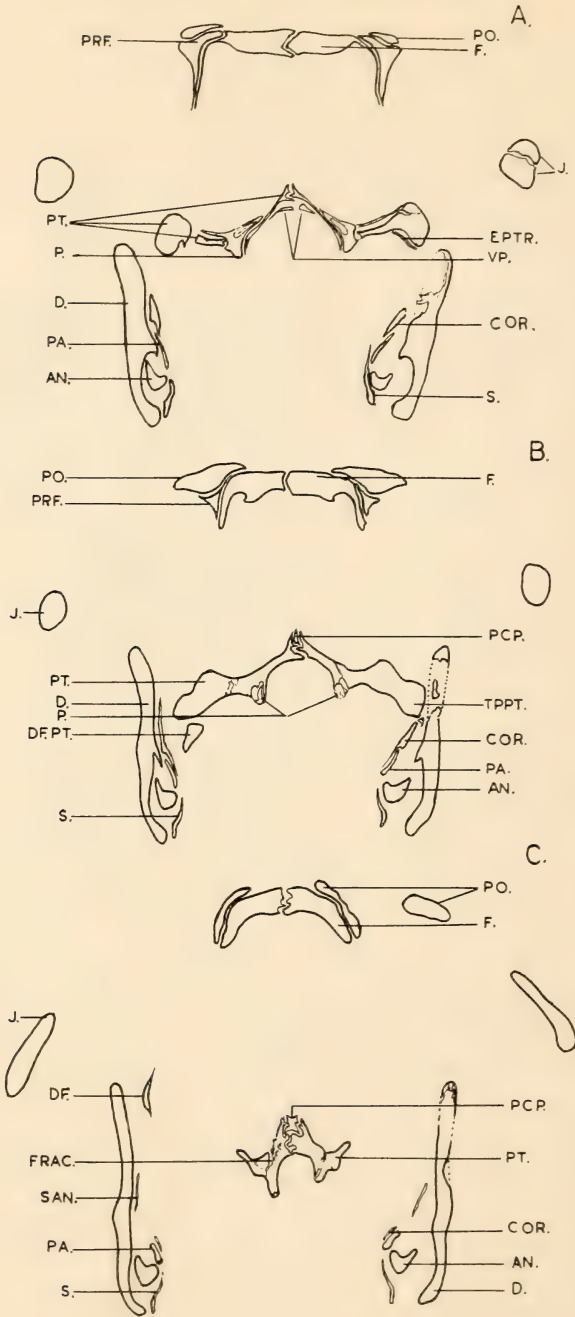


Fig. 15. Transverse sections through skull and lower jaw in orbital region. Note: A. Posterior ends of vomer and ectopterygoids and anterior ends of postorbitals; B. Posterior ends of prefrontals and palatines and anterior end of rostrum of parasphenoid; C. Relationship between pterygoids and parasphenoid rostrum behind transverse processes of pterygoids. A $\times 1,9$. B-C $\times 1,75$.

a cartilaginous internasal and interorbital septum. In the higher cynodonts the interorbital septum is apparently replaced by a presphenoid.

The ventral palatal extensions of the premaxillaries, maxillaries and palatines form a secondary palate. The vertical plate of the vomer lies above the median longitudinal suture of the palate but is not in contact with it. The two halves of the palate meet each other in a sutura harmonia. Along the median dorsal margin of each half of the palate runs a distinct ridge (see Figs 8B, 9). The secondary palate is incipient in *Gorgonopsia*, where the anterior end of the vomer is broad and flat.

In *Thrinaxodon* and higher cynodonts the development of the secondary palate is much more advanced than that of *Gorgonopsia*. The transformation of the anterior end of the vomer from a broad flat structure to a vertically orientated sheet of bone and the development of a secondary palate, without which breathing would be difficult when food was chewed, are probably related to the development of homiothermy. The secondary palate was probably necessary for a proper chewing process, which in turn was probably a prerequisite for quicker liberation of energy from the food taken in. A larger supply of energy was apparently needed in the more active advanced mammal-like reptiles. The enlarged nasal passage resulting from the development of the secondary palate was probably utilized for expansion of the surface of the mucous membrane, since the turbinates, for the presence of which there are indications (see p. 383), were probably rudimentary. Such an increased surface of mucous membrane would have been necessary to moisten and warm the increased supply of air taken in due to increased activity in those animals with increased metabolic rate and incipient homiothermy.

Brink (1957) discussed the question of homiothermy and related developments in the advanced therapsids. The nasal passage itself was possibly completely divided (but the nasopharyngeal passage only incompletely) by the vertical plate of the vomer, the probable internasal septum which appears to have rested in the groove on the dorsal edge of the vertical plate of the vomer, and an indeterminate structure between the lower end of the vomer and the palate. Possibly the ridge along the median dorsal edge of each half of the palate and the thickened lower margin of the vertical plate of the vomer indicate the attachment areas of a strong connective tissue connection between these structures.

Pterygoid (Figs 1, 6, 14B-17C)

Sectioning has revealed a considerable amount of additional information about the pterygoids. The antero-medial portion of each pterygoid is overlapped ventrally by the horizontal plate of the vomer (Figs 1, 14B, VP, KVP, PT), and the antero-lateral portion is overlapped dorsally by the palatine (Figs 14B, 15A, P, PT). It may be noted here that the structures indicated by Broom (1938a, fig. 9) as pterygoid and maxillary, are really the palatine and pterygoid respectively.

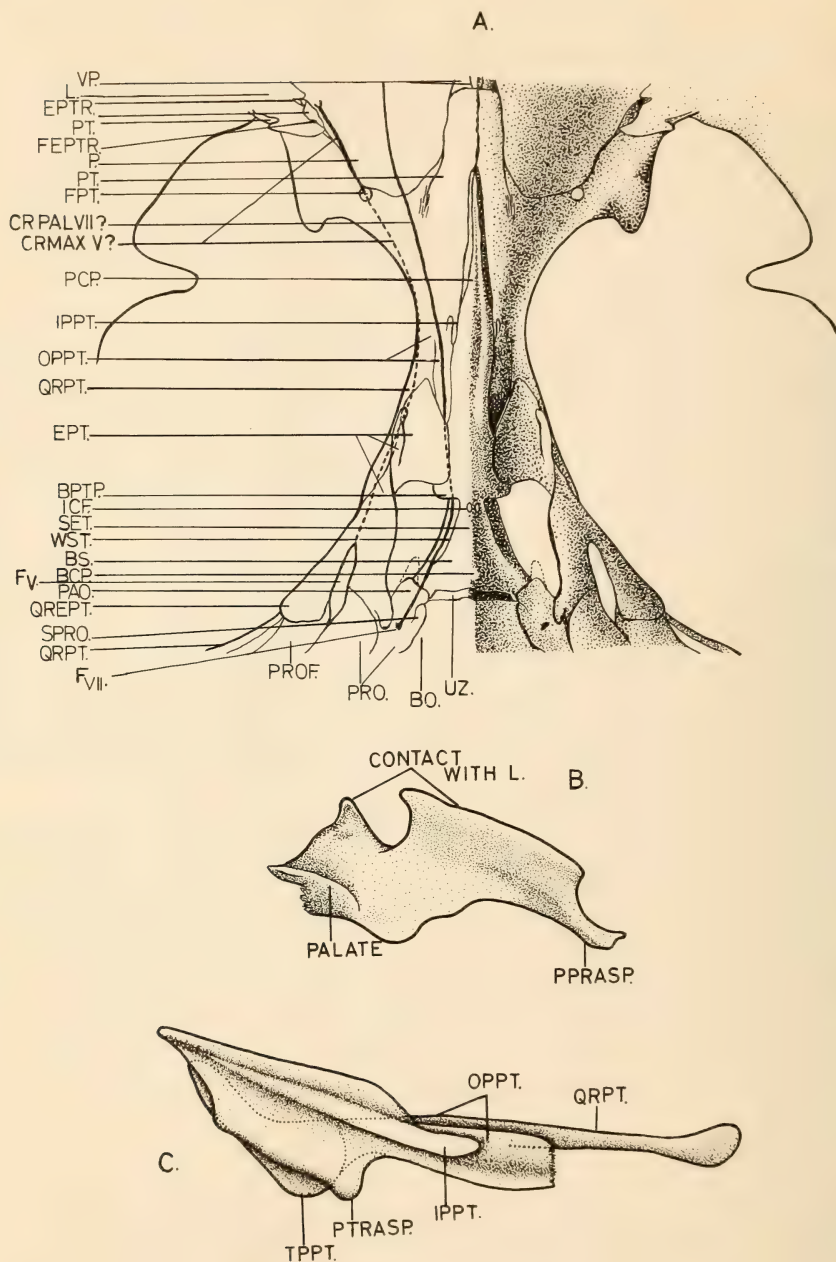


Fig. 16. Graphic reconstructions of: A. Part of palate and basicranium in dorsal view; B. Medial view of palatine; C. Medial view of pterygoid. $\times 2,5$.

The relationships of the pterygoids with the other basicranial elements behind the transverse processes of the pterygoids which guide the lower jaw (Figs 15B, 16C, TPPT) are of considerable interest because of the nature of their sutures with the parasphenoid and epipterygoids. The rostrum of the parasphenoid (Figs 15B, C, 16A, 17, PCP) lies between the posterior extensions of the pterygoids. These extensions have interdigitated sutures with each other and with the rostrum (Figs 15, 17, PT, PCP). Fractures reveal a similar condition in cynognathid skulls investigated by the present author. At the level where the anterior part of the rostrum appears in ventral view, each pterygoid divides into two bars (Fig. 17A, IDIOPPT; Figs 1, 16A, C, 17B, C, IPPT, OPPT).

Estes (1961) indicates very distinct interpterygoid vacuities at this level in juvenile *Thrinaxodon* skulls and suggests that in older specimens these vacuities are obscured by appression caused by their stronger pterygoid musculature. It is possible that the vacuities described by Estes are not natural structures, since he states that both the juvenile skulls investigated by him were crushed dorso-ventrally, which may have been responsible for the formation of 'interpterygoid vacuities'.

The inner bars (IPPT) which are joined to the rostrum by interdigitated sutures (Fig. 17B) extend back for 5 mm (Figs 1, 16C). Broom (1938, fig. 12) mistook these inner bars for the epipterygoids. In a posterior direction the inner bars taper to points which fit into shallow pits in the rostrum of the parasphenoid (Fig. 17C) exactly as described by Olson (1944). About 1.5 mm behind the division of the pterygoid, the outer bar (OPPT) widens outwards and upwards to support the anterior ventral tip of the epipterygoid (Figs 1, 16A, 17B, EPT) which rests in a groove on this outer pterygoid bar. In section this tip of the epipterygoid rapidly expands in a posterior direction to form a distinct antero-ventral process of the epipterygoid (see Fig. 22). This part of the epipterygoid appears to agree closely with the same structure in *Oligokyphus* (Kühne 1956: 55, pl. 10, fig. 1b).

The widened outer pterygoid bar divides into two about 5 mm behind the initial division of the pterygoid into an inner and an outer bar. The quadrate ramus of the pterygoid (QRPT) separates from the dorso-lateral part of the outer pterygoid bar (Figs 1, 16A, C, 17C). The remaining median part of the outer pterygoid bar extends back only 1 mm behind the division before it meets the basisphenoid in a serrated suture (Fig. 1, PTPSS).

Parrington (1946) describes ridges on the ventral surfaces of the pterygoids which continue on to the basisphenoid. The present investigation shows that a ridge extends backwards from the posterior part of each palatine, on to the pterygoid and finally on to the basisphenoid. The anterior palatine-pterygoid part of the ridge (Fig. 1, PPRASP) has been described as a ridge for the attachment of the soft palate, an identification which should probably be extended to include the more posterior part of the ridge formed by the pterygoid only (PTRASP), but this interpretation results in the assumed presence of a very long, soft palate. The pterygoid part of each ridge is formed by the median

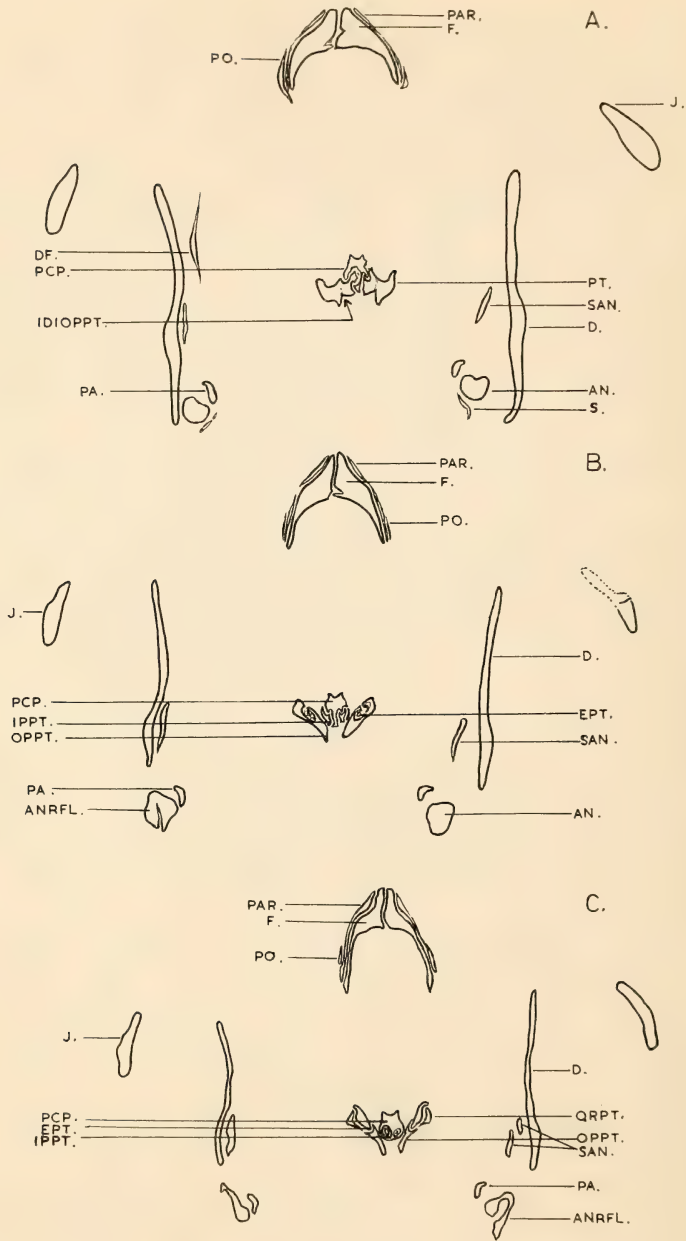


Fig. 17. Transverse sections through skull and lower jaw showing relationships: between frontals, parietals and postorbitals; between pterygoids, epipterygoids and parasphenoid rostrum; between elements of lower jaw.

A \times 1,8. B \times c 1,7. C \times 1,5.

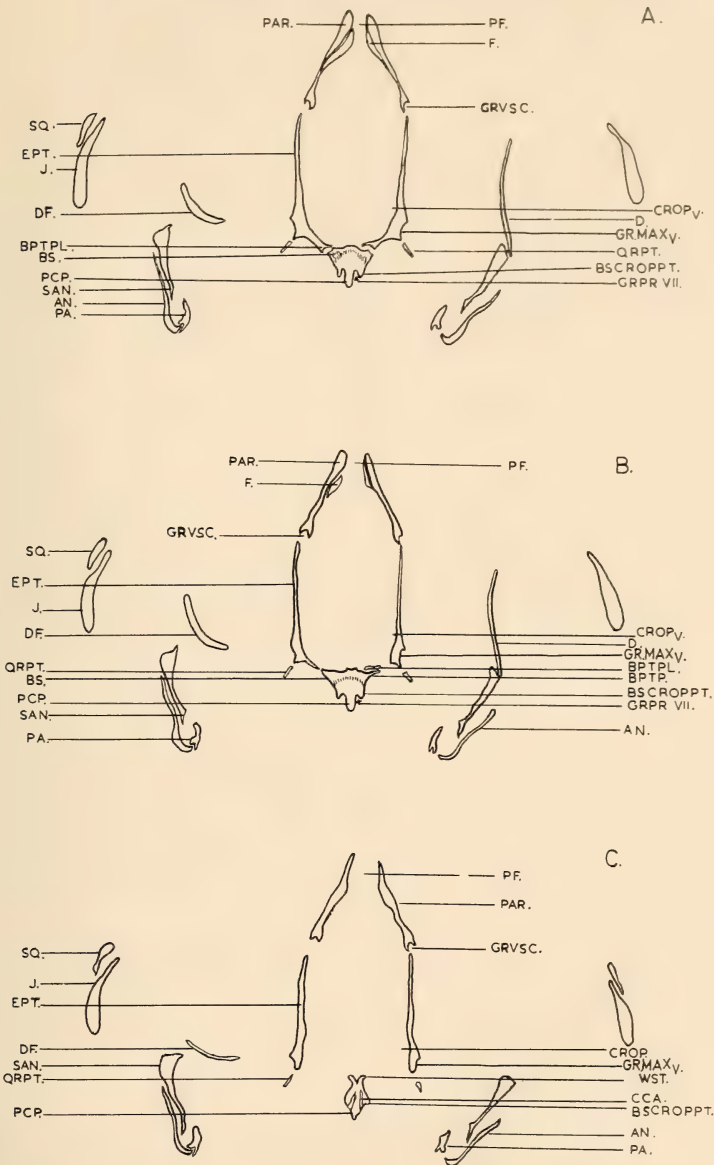


Fig. 18. Transverse sections through braincase and lower jaw showing parietal foramen, relationships between parietals, epipterygoids and basi-sphenoid and between carotid canals and sella turcica. Note surangular, angular and prearticular relationships. $\times 1,5$.

ventral part of the outer pterygoid bar and its posterior end by a ridge on the basisphenoid (Figs 18A, B, C, BSCROPPT) just lateral to the keeled posterior part of the parasphenoid rostrum (see Fig. 1). The basisphenoid part of the ridge forms the median ventral margin of the basiptyergoid process (Fig. 1, BPTP).

Between the keeled posterior part of the parasphenoid rostrum (Parrington's (1946) 'ridge on the processus cultriformis') and the closely applied median ventral part of the outer pterygoid bars, deep grooves are formed. These grooves continue backwards on to the ventral surface of the basisphenoid (Figs 1, 18A, B, GRPR_{vii}) as far as the internal carotid foramina (Fig. 1, ICF). Olson (1944) suggested that the rami palatini of the facial nerves passed forward in these grooves and then turned upwards between the pterygoids and basisphenoid, anterior to the basiptyergoid processes. Parrington (1946) questioned this suggestion because he thought that Olson did not show clearly where the nerve re-entered the skull. This uncertainty apparently rests on a misunderstanding of Olson's description. The point of re-entry could lie in the fork between the inner pterygoid bar (suturally joined to the rostrum) and the outer pterygoid bar (Figs 1, 16A) in what may be, according to the description of Estes (1961), the remnant of the interptyergoid vacuity. The canal is difficult to see without sectioning, because the ventral parts of the outer pterygoid bars are inclined towards each other (Fig. 17B, C, OPPT). A similar condition exists in the cynognathids which were investigated. In these forms the probable course of the ramus palatinus of the facial nerve can easily be followed forward from its exit from the braincase.

Parrington (1946) suggested that a small foramen which he found only in one specimen on the left side between the basiptyergoid process and the pterygoid might have transmitted the ramus palatinus. The actual relationships between the bones, as determined by sectioning, differ somewhat from those figured by Parrington, and the foramen probably represents a small opening in the suture between the two elements.

Probably the ramus palatinus of the facial nerve passed through the pterygoid-parasphenoid canal described above (Fig. 16A, CRPAL_{vii}). From here it may have passed backwards lateral to the internal carotid foramina, on to the upper half of the lateral face of the basisphenoid. In the region of the unossified zone it may have passed on to the concave lateral face of the prootic on which it probably ran gradually upwards. It probably passed below the lateral lamina of the prootic (PROF) and entered its foramen which is situated just below and behind the large foramen for the trigeminal nerve. The maxillary ramus (Figs 1, 16A, CRMAX_v) of the trigeminal nerve after leaving the 'maxillary antrum' probably continued in the groove on the dorsal surface of the pterygoid until it penetrated the foramen pterygoideum (FPT). From here it probably continued along the latero-ventral surface of the outer prong of the pterygoid (OPPT) until the latter's quadrate ramus (QRPT) separated and the antero-ventral process of the epiptyergoid became laterally exposed. From this point the

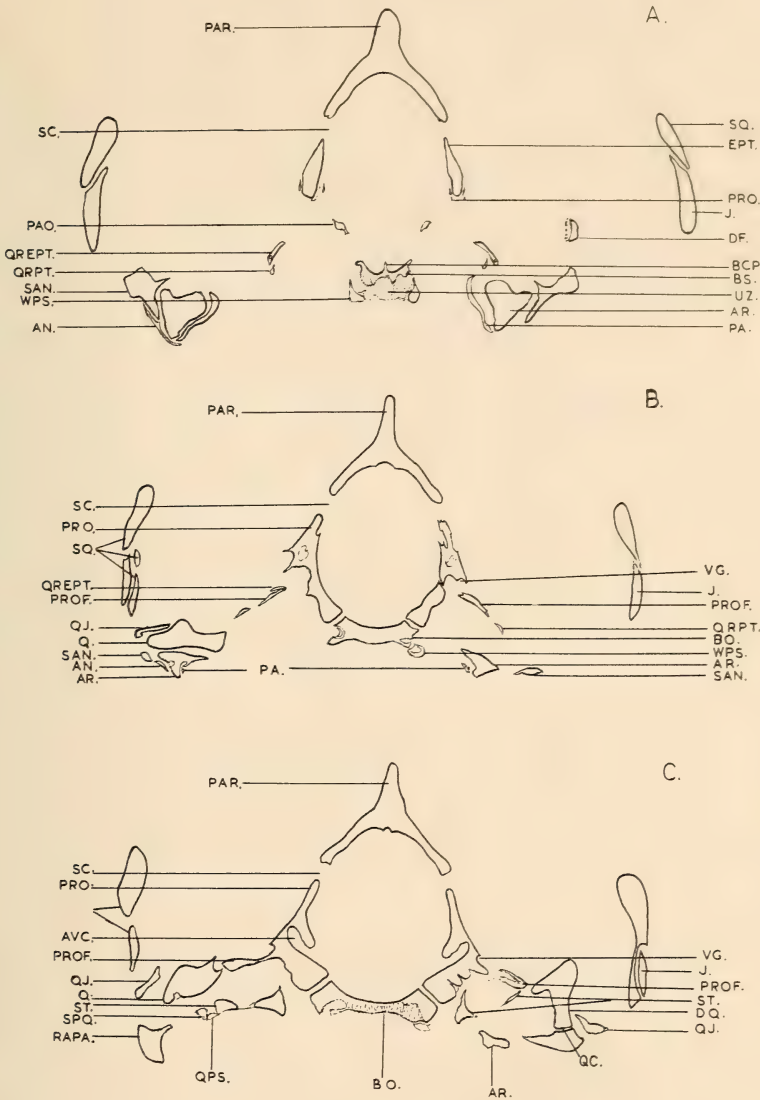


Fig. 19. Transverse sections through braincase and lower jaw. A. Trigeminal foramen, tips of pila antotica and antero-dorsal process of prootic and unossified zone in basicranium. B. Suspensorial region and lateral lamina of prootic. C. Retroarticular process of articular, anterior vertical semicircular canal of internal ear, and relationships between lateral lamina, quadrate and stapes.

A × 1,7. B-C × c. 1,5.

maxillary ramus probably continued along the groove (Fig. 18, CRMAX_v) on its surface, just above the level of the quadrate ramus of the pterygoid, until it reached the ganglion Gasseri lying within the foramen (F_v) between the epipterygoid and prootic (Figs 1, 16A). The abducent nerve probably followed much the same course as the palatine ramus of the facial nerve and entered its foramen (Fig. 6A, F_{vi}) anterior to and below the foramen for the former. The geniculate ganglion of the facial nerve (VII) probably lay in the posterior part of the foramen between the epipterygoid and the prootic, in a recess under the prootic. After entering its foramen the palatine ramus of the facial nerve had only to run directly upwards for a very short distance before joining its ganglion.

Basisphenoid and parasphenoid (Figs 1, 6, 15B-16A, 17A-19B, 20, 21C, 22B, 25A, 28, 29A)

Sectioning revealed no more information than that given by Olson (1944) and Parrington (1946), and that given above under the section on the pterygoid. An unossified zone is present between the basisphenoid and basioccipital (Figs 1, 6A, 16A, 19A, 20, UZ). The parasphenoid is well developed laterally. Earlier preparation of the sectioned skull exposed the basicranium so that it is not possible to be sure exactly how far the parasphenoid extends backwards on the ventral surface. It does not cover the unossified zone and the anterior part of the basioccipital, but this may be due either to damage or to the fact that the specimen is fairly young (Fig. 1, WPS).

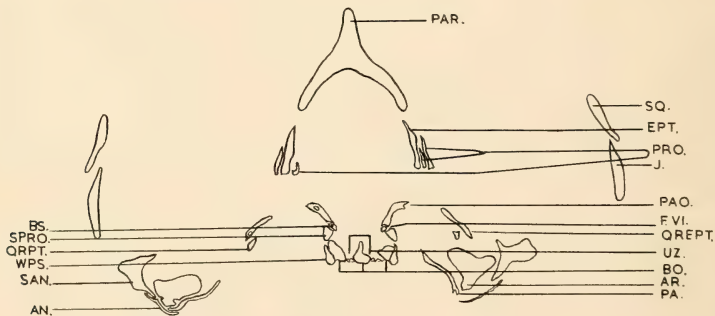


Fig. 20. Transverse section through braincase and lower jaw showing relationship between epipterygoid and prootic, abducent foramen (see also Figs 21C and 24A), and unossified zone in basicranium. $\times 1.5$.

In ventral view the wings of the parasphenoid do not extend as far laterally towards the fenestra ovalis as they are figured by Parrington (1946). Again the difference may be ascribed to different stages of growth, since Estes (1961) also figures the posterior ends of the wings of the parasphenoid in very young specimens as lying comparatively farther forward than shown by Parrington. The dorsum sellae is practically non-existent and therefore the sella turcica (SET) is very shallow and narrow and flanked laterally by thin bone walls

(Figs 16A, 21C, SET, WST). The internal carotid canals emerge almost directly above their points of entry into the parasphenoid-basisphenoid (Figs 1, 16A, ICF; 18C, CCA).

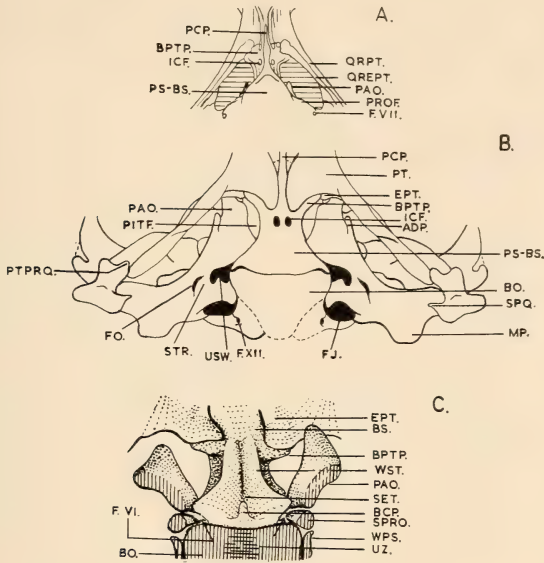


Fig. 21. A. Ventral view of part of basicranium (after Parrington 1946) showing pila antotica and basipterygoid process. B. Ventral view of basicranium of a scaloposaurid (after Crompton 1955*b*) for comparison with A. C. Postero-dorsal view into braincase of enlarged wax reconstruction of serially sectioned skull showing shallow sella turcica, basicranial process, abducent foramen and pila antotica. C \times 2.5.

The parasphenoidal teeth described in juvenile *Thrinaxodon* specimens by Estes (1961) may be similar to the irregular surface of the thickened medio-ventral margin of the maxillary and palatine in cynodonts. The median bony ridge thus formed appears comparable with the raphe palati of the mammalian palate. Seeley (1908) described the irregular surface of the maxillary and palatine as a dental armature and Watson (1911) referred to granules with enamelled tips. Broom (1911) and Broili & Schröder (1934*a*) rejected these descriptions. The present author regards the irregular surface of the median ridge as part of the attachment for a mucous membrane which had to be firmly fixed so that forceful movements of the tongue would not dislodge it. In mammals the lamina propria of the mucous membrane is usually continuous with the periosteum of the bone above. Laterally the mucous membrane is not evenly adherent to the bone and is connected to it by strong bundles of connective tissue. The epithelium of the hard palate, which has to be able to withstand wear and tear, is

attached to the median 'raphe' by a thin lamina propria. Rugae with connective tissue cores radiate laterally from the raphe, the uneven surface of which may serve to aid in the attachment of the connective tissue cores (to the periosteum).

A small foramen, described by Estes (1961) and confirmed by the current investigation, lies in each wing of the parasphenoid just medial to the fenestra ovalis and anterior to the opisthotic contact with the basioccipital (Figs 1, 25A, FN₁). This foramen is situated in the precise position where the mammalian Eustachian tube opens.

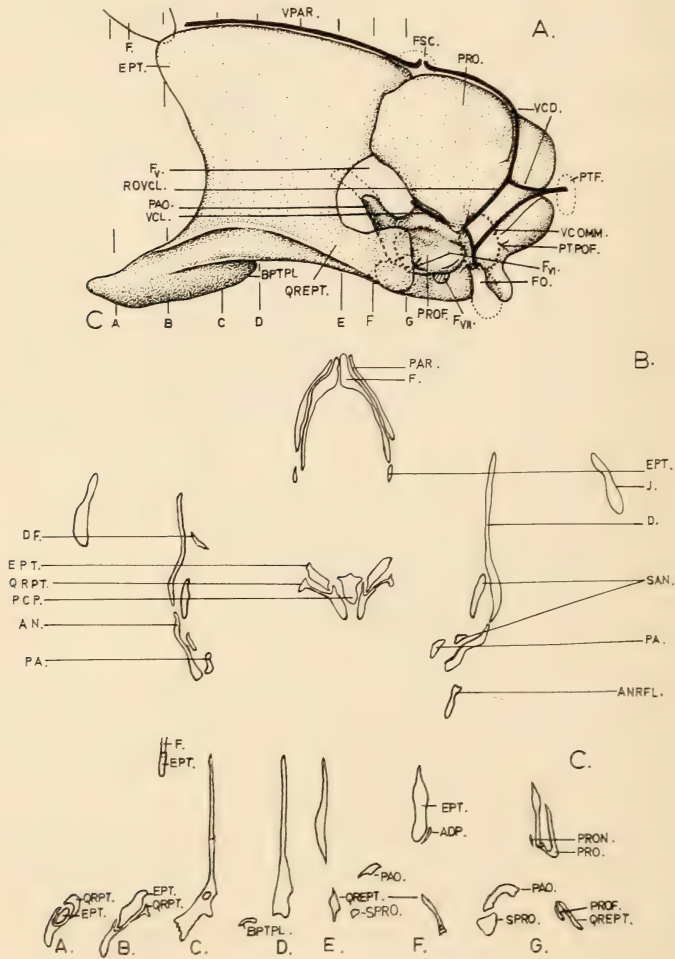


Fig. 22. A. Graphic reconstruction of epipterygoid and prootic in lateral view to show probable system of veins, contact with frontal, and levels of sections given in C. B. Transverse section showing frontal-epipterygoid contact, detaching quadrate ramus of pterygoid and postdentary bones of lower jaw. C. Sections indicated in A. A \times 3. B \times 1,5. C \times 2,1.

Epipterygoid (Figs 1, 6A, B, 16A, 17B-19B, 20-22, 28)

The only feature of this bone which has not been described in earlier publications is the relationship of the tip of its antero-ventral process to the pterygoid, described above under Pterygoid (p. 359). The slight overlap of the frontal and epipterygoid (Figs 1, 6A, B, 22A, B, C) is a feature also found in the cynognathid skull and it is described by Crompton (1958) in *Diarthrognathus* as well. In *Thrinaxodon* the anterior part of the lateral flange of the frontal is laterally overlapped by the prefrontal (Figs 6, 15A, B, F, PRF). The anterior part of the postorbital in turn partly overlaps the posterior end of the prefrontal, but actually lies mainly dorsal to the bone (Fig. 6B, PO, PRF). Further back the lateral flange of the frontal is laterally overlapped by the thin front end of the parietal of which the lower part in turn is laterally overlapped by the posterior end of the postorbital (Figs 6, 17, PAR, PO). Between the posterior end of the prefrontal and the anterior end of the parietal only the postorbital overlaps the frontal flange. Behind the postorbital only the thin parietal sheet overlaps the frontal flange (Figs 6, 18A, B). At this level the frontal forms the anterior and lateral lower margins of the wall of the parietal foramen (PF). In sections the posterior lower part of the lateral flange of the frontal anterior to the parietal foramen becomes progressively longer, until its lower end makes contact with the anterior upper edge of the epipterygoid (Figs 6, 22, F, EPT). This ventrally projecting part of the frontal ends well in front of the upper part of the bone and the parietal foramen. In this region the lower end of the frontal flange protrudes well below the parietal which overlaps its dorsal part (Fig. 6B).

Sectioning, therefore, shows that it is not just a slender horizontal process of the frontal which meets the epipterygoid. The median wall of the orbit is formed in the same way in the cynognathids and *Diarthrognathus*, and closely resembles the condition in mammals and tritylodontids.

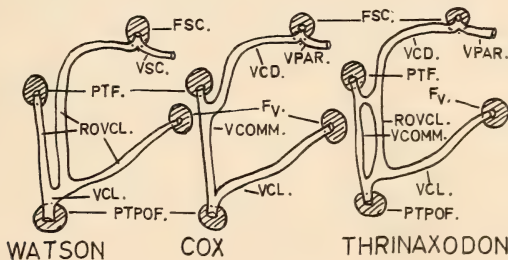


Fig. 23. Three diagrams to show various interpretations of venous system around braincase. $\times c. 2.5$.

Prootic (Figs 1, 2, 6, 16A, 19A-22A, 22C-24A, 25A, 26, 27, 29A, B)

The anterior part of the prootic consists of the antero-dorsal process (ossified taenia marginalis, Crompton 1955b) which forms the postero-dorsal margin of the trigeminal foramen (Figs 22A, 24A, ADP), and the antero-ventral process, identified by Parrington (1946) and Crompton (1955b) as an

ossification of the pila antotica (PAO) which forms the postero-ventral margin of the trigeminal foramen. The postero-dorsal part of the epipterygoid, which forms the antero-dorsal margin of the trigeminal foramen, projects on to the anterior part of the antero-dorsal process to which it is joined by a serrated suture. It is held between a large outer plate and a slender inner process (Figs 6A, 22A, 28, ADP). The notch described by Olson (1944: 16-17), dorsal to both the prootic incisure and the latero-dorsal process, is closed off by the lower margin of the parietal to form the foramen for the vena capitis dorsalis (Figs 6A, 22A, FSC) (see also pp. 373-5).

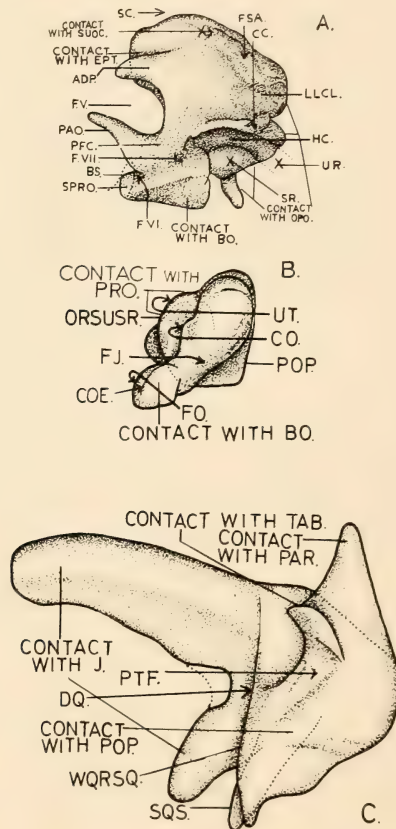


Fig. 24. Graphic reconstructions of medial views of: A. Prootic; B. Opisthotic; C. Squamosal. $\times 2,5$.

Some detail can be added to the descriptions by Olson (1944) and Parrington (1946) of the foramen for the abducent nerve. The nerve passes through a deep notch in the antero-ventral edge of the antero-ventral process (pila antotica) (Figs 20, 21C, 24A, F_{vi}). The notch is closed anteriorly by a postero-dorsally

directed flange of the lateral wall of the sella turcica which lies in the dorsal surface of the basisphenoid (Figs 6A, 16A, 21C, BS, WST, F_{vi}). Olson's (1944) figure is therefore more closely comparable with the structure as determined in the present investigation than Parrington's (1946) figure in which the foramen lies entirely within the antero-ventral process.

Sectioning shows that the foramen lies behind the sella turcica and the unossified zone. The foramen for the facial nerve (Figs 24A, 27, 28, F_{vii}) is quite distinct immediately below and behind the prootic incisure (posterior wall of the trigeminal foramen) from which it is separated by the prefacial commissure. The ramus ophthalmicus profundus of the trigeminal nerve probably ran forward along the medial surface of the lower third of the epipterygoid from the Gasserian ganglion lying just within the trigeminal foramen. Its possible course is indicated by a slight though definite groove on the medial surface of the epipterygoid just above the level of the antero-ventral process of this bone. On emerging from the braincase through the lower end of the foramen lacerum anterium (Fig. 6A, FLA), the ramus ophthalmicus profundus would have been immediately above the anterior ventral part of the epipterygoid (Fig. 18, CROP_v) which is in contact anteriorly with the pterygoid, and more posteriorly with the basisphenoid (Fig. 18B, BPTPL).

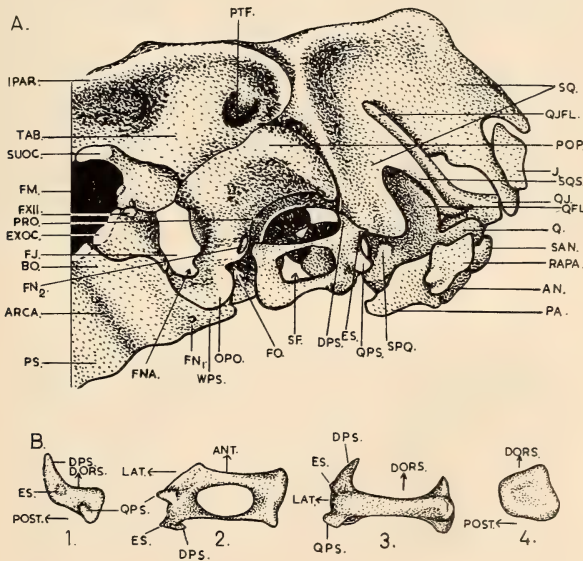


Fig. 25. A. Antero-ventral view of posterior part of enlarged wax reproduction of serially sectioned skull to show contacts of stapes and quadrate. Note retroarticular process of articular. B1, 2, 3, 4. Lateral, ventral, anterior and medial views of right stapes. Note positions of anterior, dorsal and posterior planes in the different views. $\times 2.5$.

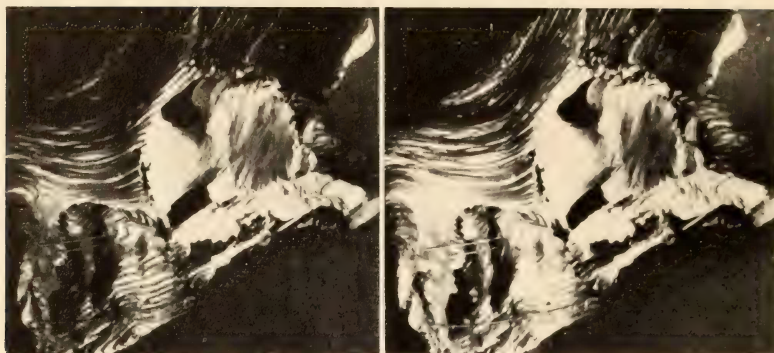


Fig. 26. Stereophotograph of anterior view of right posterior part of model of serially sectioned skull showing squamosal recess with quadrate and quadratojugal, as well as outer surface of prootic with grooves and canals for system of veins. Approximately $\times 3$. (See also Fig. 22A.) See accompanying diagram for lettering.

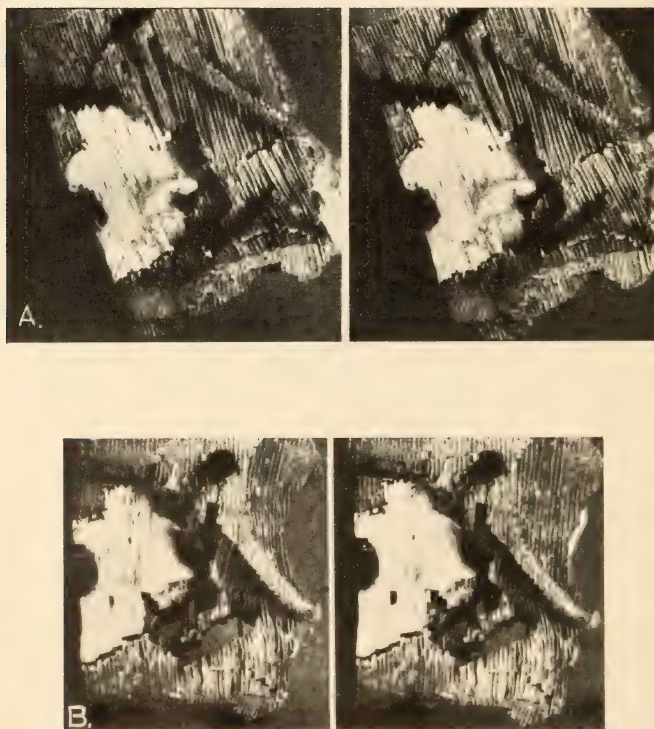


Fig. 27. Stereophotographs of: A. Inner surface of wall of right side of braincase; B. Floor and ventrally situated structural features (jugular foramen, sacculo-cochlear recess and fenestra ovalis). Approximately $\times 2,5$. See accompanying explanatory diagrams for lettering. (See also Figs 24A, 28.)

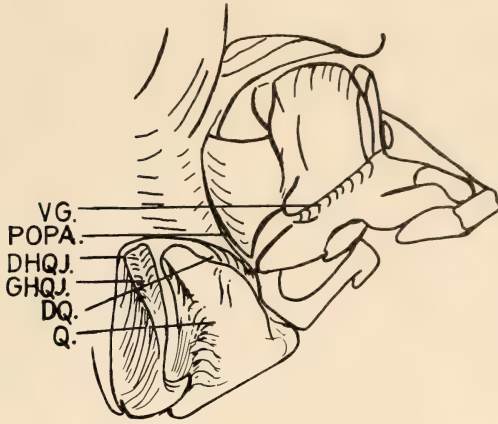


Fig. 26. Explanatory diagram.

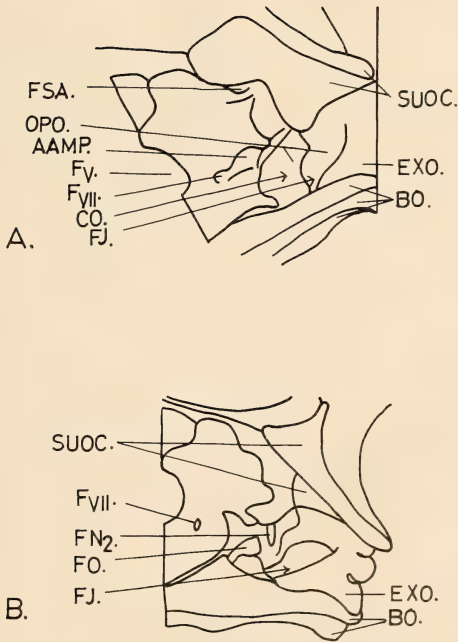


Fig. 27. Explanatory diagram.

The paroccipital process is formed by a postero-lateral flange of the prootic (see Fig. 26) which rests dorsally on the opisthotic in a squamous suture (Fig. 29B, PRO, POP, OPO). It abuts against the squamosal with only its dorsal and ventral margins, but possibly had a cartilaginous cap which became ossified during later stages of growth than that represented by the sectioned skull. The step-like suture described by Parrington, between the prootic and opisthotic (Figs 1, 25A, POP, PRO) which forms part of the roof and the hind wall of the middle ear cavity, is confirmed. The prootic flange (lateral lamina) (PROF) forms the anterior border of the pterygo-paroccipital foramen (Fig. 2, PTPOF) and meets the quadrate rami of the pterygoid and epipterygoid (Figs 1, 2, 16A, 19B, 22A, QREPT). The lateral lamina of the prootic and the quadrate ramus of the pterygoid extend to the median margin of the quadrate (Figs 1, 17C, 26, Q).

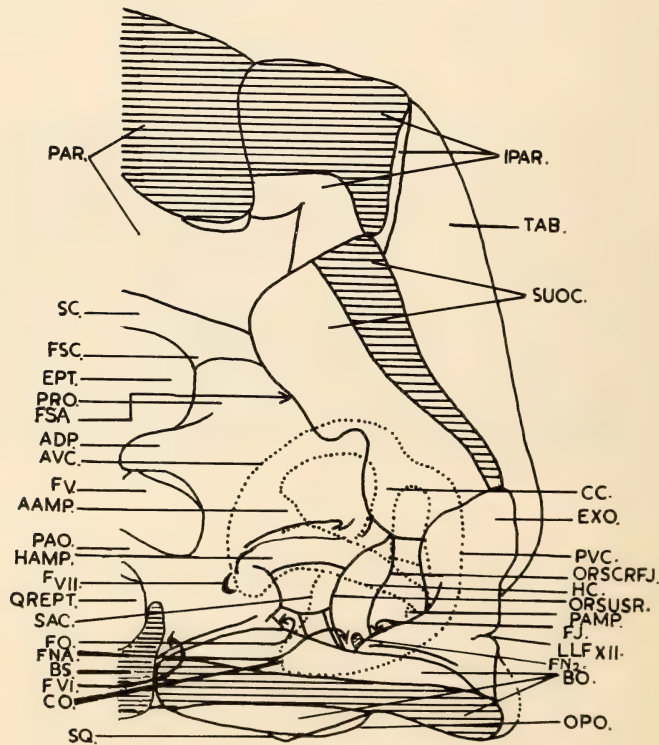


Fig. 28. Graphic reconstruction of inner ear structures in relation to the otic and occipital bones. $\times 4$.

The subarcuate fossa is very distinct (Figs 24A, 27, 28, FSA). In an oblique dorsal view backwards into the braincase this excavation for the lateral lobe of the cerebellum appears to extend into a large space above the anterior opening

of the posttemporal fossa. There appears to be no vascular duct which penetrates the cranial wall from the subarcuate fossa as there is in *Oligokyphus* (Kühne 1956). (See, however, under Supraoccipital, p. 378.) A convexly curved horizontal lamina separated the excavation for the lateral lobe of the cerebellum from the horizontal canal and the vestibule (Fig. 27A). This lamina is also described by Brink (1955a, fig. 2b) for *Diademodon*, in which the conditions in this part of the braincase agree very closely with those in *Thrinaxodon*. The relationship of the semicircular canals to the subarcuate fossa can be seen in Figure 28.

The most interesting feature of the otic bones is the system of grooves, canals, and foramina for veins which enter and leave the braincase and was described by Watson (1920) and Parrington (1946). In a study of the dicynodont *Kingoria*, Cox (1959) pays considerable attention to these veins. Since the system of grooves, canals, and foramina in *Kingoria* appears to be closely comparable with that of *Thrinaxodon* and of the cynognathids, Cox's interpretations, with those of the earlier investigators, are of considerable value for understanding the conditions in *Thrinaxodon*. Cox suggests that the groove (Fig. 18, GRVSC) along the junction of the parietal and epipterygoid of cynodonts represents the course of the vena parietalis, and the foramen (Figs 6A, 22A, 28, FSC, 26, 27) described by Watson (1911, 1920) between the parietal and prootic is the point of entry into the braincase of the vena parietalis and the vena capitis dorsalis (Watson's 'vein of sinus canal') which, according to Cox, drained forward from the occipital musculature. The course of this latter vein was through the posttemporal fossa, then upwards into the posterior end of the dorsal groove (sinus canal), and into the braincase through the above-mentioned foramen. The vena capitis lateralis ran between the pterygo-paroccipital foramen (Figs 22A, 23, PTPOF, 26) and the trigeminal foramen. The vena capitis dorsalis and the vena capitis lateralis were joined by a vein which ran forward across the dorsal and anterior surfaces of the paroccipital process from the posttemporal foramen into the pterygo-paroccipital foramen, to provide an alternative method of drainage. Cox's interpretation is a modification of Watson's (1920) and is supposed to allow for the fact that the vein which occupied the posttemporal fossa drained forward.

In Watson's interpretation, which is made difficult because it gives a wrong impression of the direction of flow of the blood, the vena capitis lateralis ran through the pterygo-paroccipital foramen and was formed by three roots. These were: one which ran forward through the posttemporal fossa; one which ran backwards from the trigeminal foramen; and one which ran backwards in and then downwards and forwards from the 'sinus canal' which is the groove along the ventral parietal and dorsal prootic and epipterygoid borders. Watson also described two smaller veins. The first is said to have left the braincase through a foramen between the prootic and parietal and then to have joined a vein which ran in the 'sinus canal'. According to Cox this foramen is for the vena parietalis and the vena capitis dorsalis. The second small vein described by

Watson is said to have left the braincase through the upper part of the foramen for the trigeminal nerve and then to have joined the third root of the vena capitis lateralis which ran from this same foramen.

A study of the skull of *Thrinaxodon* reveals that the grooves and canals fit the interpretation of Watson (1920) of the courses of the main veins as well as they do that of Cox (1959) and that the correct interpretation may be a synthesis of the two interpretations. Figure 26 shows a very distinct groove (VG) running between the pterygo-paroccipital foramen and the trigeminal foramen. Both Watson and Cox agree that a vein ran along this groove, Watson calling it a root of the vena capitis lateralis, and Cox calling it *the* vena capitis lateralis. The structure of the anterior dorsal face of the paroccipital process leaves no doubt that a vein ran across it (see Fig. 26) between the posttemporal fossa and the pterygo-paroccipital foramen. This vein must have been the second root of the vena capitis lateralis described by Watson and which is regarded by Cox as a communicating vein between the vein which he calls the 'vena capitis dorsalis' and the vein which he calls the 'vena capitis lateralis'.

In order to understand the course of Cox's vena parietalis and vena capitis dorsalis, and Watson's vein of the sinus canal, it is necessary to describe briefly the relationship between the lower margin of the parietal and the upper margins of the epipterygoid and prootic.

In the reconstructed skull of *Thrinaxodon* the parietal and the epipterygoid do not make contact and the anterior part of Watson's sinus canal is therefore not distinct (Fig. 6A, EPT). Since the lower margin of the parietal is, however, grooved (Fig. 18, GRVSC) it is possible that the epipterygoid and the anterior part of the prootic are slightly dislocated from the parietal, or else that further growth would have formed the groove or canal proper. The posterior part of the groove (canal) is normal in the reconstructed skull where it is walled medially by the anterior end of the supraoccipital (Figs 6A, 29A, SUOC).

Watson believed that a third root of the vena capitis lateralis ran along this groove, but Cox believes that its anterior part was occupied by the vena parietalis and its posterior part by the vena capitis dorsalis. The further course of the vein which occupied the posterior part of the groove (or canal) can easily be followed in the reconstructed skull where a distinct groove runs straight downwards from the horizontal groove, well in front of the eaves formed by the squamosal over the posttemporal fossa (Figs 22, VCD, 26). It then continues forwards and downwards on the paroccipital process at its proximal end where it is continuous with the wall of the braincase. Watson's description and figure of the course of the third root of the vena capitis lateralis fit the groove described above very well. Cox's description of the upper part of the groove is also correct, because at the base of the vertical part of the groove where it turns forwards there is an equally distinct part of the groove which turns backwards (Figs 23 *Thrinaxodon*, 26) into the posttemporal fossa. This must be the course of the posterior part of Cox's vena capitis dorsalis. There is no doubt that the vein which ran down the paroccipital process (see p. 373) splits from Cox's vena

capitis dorsalis in the posttemporal fossa because their grooves merge into a single large groove.

The reconstructed *Thrinaxodon* skull also distinctly shows that the third root of the vena capitis lateralis (Watson) joined the one from the trigeminal foramen at the termination of the groove (VG) for the latter vein at the dorsal margin of the pterygo-paroccipital foramen where a distinct lamina of the prootic protects the confluence (Figs 22A, 26).

It appears therefore that:

- (a) the upper end of the third root of the vena capitis lateralis with its own root from the posttemporal fossa is Cox's vena capitis dorsalis;
- (b) the lower end of the third root of the vena capitis lateralis which is not recognized by Cox is present;
- (c) the second root of the vena capitis lateralis which came through the posttemporal fossa to the pterygo-paroccipital foramen is the communicating vein of Cox, and
- (d) the first root of the vena capitis lateralis which ran towards the trigeminal foramen is the vena capitis lateralis of Cox.

The interpretations of Watson (1920), Cox (1959) and the present one for *Thrinaxodon* are compared diagrammatically in Figure 23.

Parietal (Figs 6, 17A–20, 22B, 28, 29)

The relationships of the parietal with the frontal and postorbital have been described above (see Epipterygoid, p. 367). In this region the parietal (PAR) is a thin sheet of bone (Figs 17A–18C). Further back, behind the frontal, the parietal is thicker in section and along its lower end, which almost reaches the upper margin of the epipterygoid, runs the groove for the vena parietalis (Cox 1959) (Fig. 18, GRVSC). Behind the parietal foramen, which is about 4 mm in length, the two parietals are fused and appear in sections as a triradiate structure, the dorsal limb of which forms the parietal crest (Figs 19, 20, 28, 29A, B). Still further back the groove along the lower margin of the parietal disappears. The lower margin of the parietal becomes rounded for a distance of about 6 mm and is separated from the upper borders of the epipterygoid and prootic by an interspace of about 1 mm (Figs 19, 20, 29A) which may be the result of a dislodgement of the bones, or may represent a growth feature which would have disappeared later. Along the posterior dorsal part of the 'sinus canal' between the parietal and prootic the considerably expanded lower end of the parietal and the similarly expanded upper part of the prootic are again distinctly grooved (Fig. 29A, PAR, PRO). In this region the anterior end of the supraoccipital forms the inner wall of the canal (Fig. 26) which now turns downwards and outwards.

Basioccipital and Exoccipital (Figs 1, 6, 16A, 19B–21, 25A, 27–29C)

Very little can be added to the previous descriptions by Olson (1944) and Parrington (1946). Each exoccipital (EXO) meets the supraoccipital (SUOC) in the sectioned skull in a sutura squamosa (Figs 6A, 28). An antero-ventral extension of the exoccipital lies on the latero-dorsal surface of the posterior part

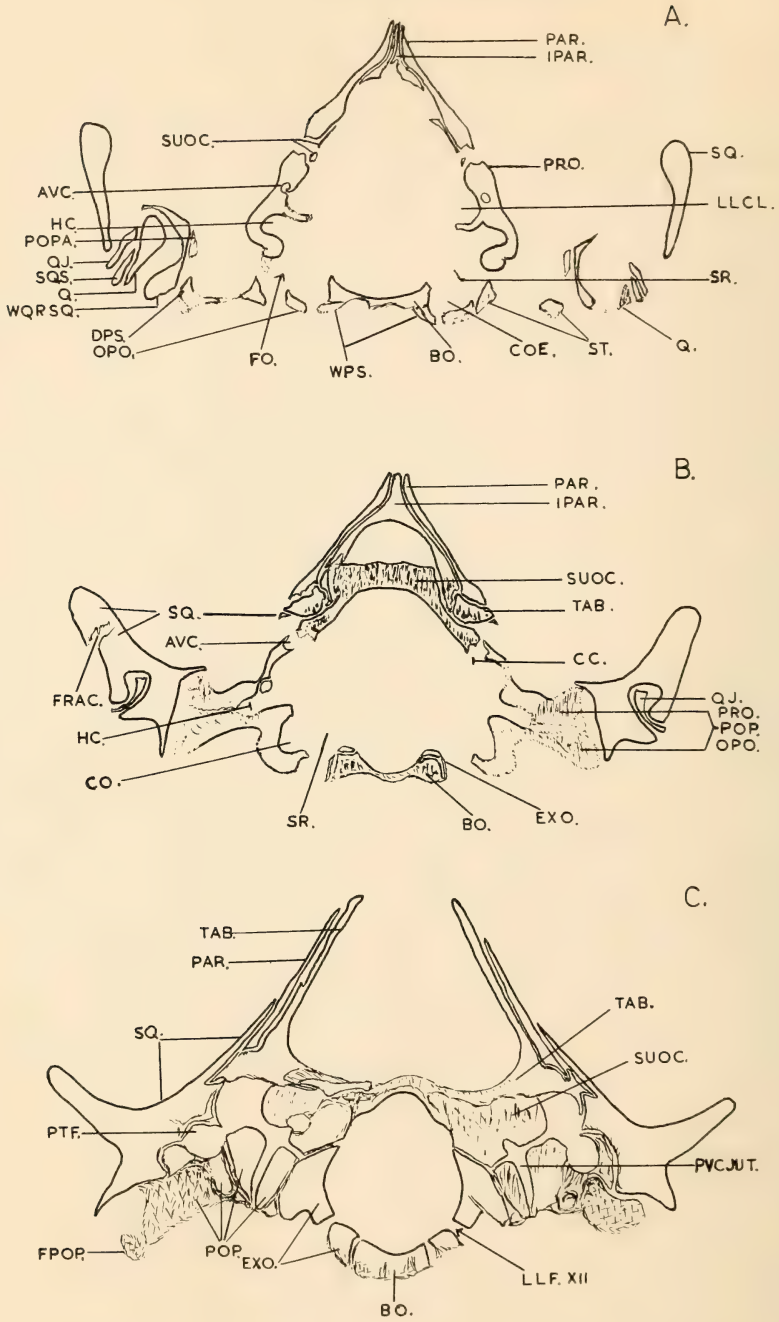


Fig. 29. Transverse sections through posterior part of braincase and occiput to show relationships of constituent bones. Structures accommodating inner ear are indicated. A \times 1,5. B \times 1,6. C \times 2,5.

of the basioccipital (Figs 6A, 27, 28, 29B, C, EXO, BO) where it forms the inner wall of the jugular foramen. Two distinct foramina (Figs 1, 6A, F_{xii}) penetrate the exoccipital. The lower one (LLF_{xii}), which is the larger of the two, leaves the braincase almost in the foramen magnum, and practically below the jugular foramen. The smaller upper foramen lies along the posterior part of the first foramen, but lateral to it, and may have given passage either to a second hypoglossal branch, or to a vein (see Figs 27B, 28).

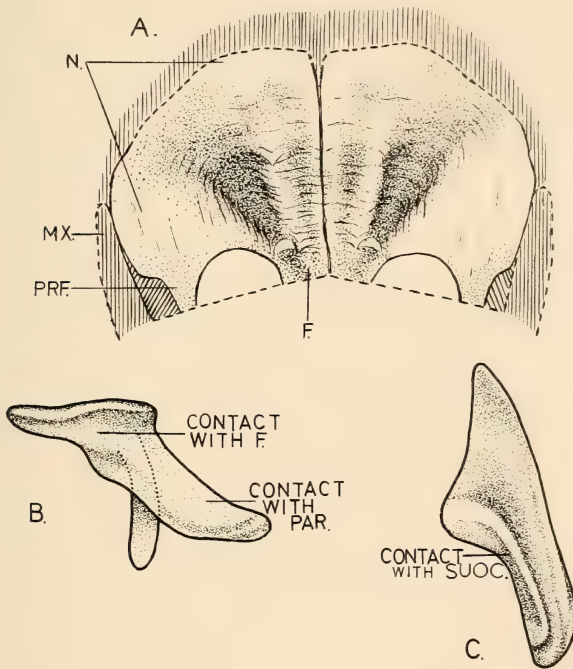


Fig. 30. A. Inner view of roof of snout of enlarged wax reproduction of serially sectioned skull to show series of ridges and depressions probably for attachment of turbinals. B-C. Graphic reconstructions of medial views of postorbital and tabular respectively. $\times 2,5$.

Supraoccipital (Figs 1, 6A, 25A, 27-29)

Mention has been made of the dorso-lateral parts of the supraoccipital (Figs 6A, 28, 29A, SUOC) which extend forward about 2,6 mm beyond the median dorsal shelf on each side of the skull along the upper border of the prootic and the lower border of the parietal. The supraoccipital is a trough-shaped bone which lies tilted back at an angle of about 45 degrees (Figs 6A, 27, 28). The base of the trough forms the roof of the cerebellar part of the braincase and the walls of the trough, which become thicker backwards (Fig. 29A, B), take part in the formation of the walls of the braincase. The anterior upper part of the roof

is considerably expanded in vertical diameter (Figs 6A, 27B, 28). Above this expanded anterior upper end of the supraoccipital, below and in front of the interparietal is an open space about 3 mm in height and about 2 mm in length (Figs 6A, 27B, 28, 29B, IPAR, SUOC). Its maximum anterior width is about 4,5 mm, but it becomes narrower further back. Such a space is also found in the cynognathids investigated, as well as in *Diademodon* (Brink 1955a), but its function is uncertain. Brink suggests that in the live animal a cartilaginous extension of the supraoccipital filled the space. The lower ends of the interparietal come down laterally alongside the expanded anterior part of the supraoccipital shelf (Figs 6A, 28, 29B, IPAR, SUOC) against which they are held by the parietal flanges which completely cover them in lateral view (Figs 6B, 29B, IPAR, PAR). The anterior extensions of the tabulars (Fig. 30C) lie below the lower ends of the interparietal and medio-ventral to the lower ends of the parietals (Fig. 29B, TAB). In lateral view they are exposed for a distance of about 2,2 mm before being covered by the squamosal. This bone forms a roof (Figs 2, SQ, 26) which probably protected the blood-vessels, emerging from the posttemporal fossa, against constricting pressure of the temporal musculature. The anterior exposure of the tabular in the posterior end of the groove for the 'vein of the sinus canal' is also found in the cynognathids and *Diademodon*.

About half-way down its sloping anterior border on each side, the supraoccipital has a wide notch (Figs 6A, 27A, 28, SUOC). This notch is the posterior medial margin of the excavation for the lateral lobe of the cerebellum which is continued postero-laterally towards the posttemporal fossa between the posterior part of the prootic and the supraoccipital. The posterior end of the anterior vertical semicircular canal runs along the notch, but just behind its margin (Fig. 28, AVC). The anterior upper end of the posterior vertical semicircular canal runs in the outer surface of the lower end of the supraoccipital below and behind the notch (Fig 28, PVC). A groove (Figs 6A, 24A, FSA) on the inner upper surface of the posterior part of the prootic is separated from the excavation for the lateral lobe of the cerebellum (LLCL) just below it by a distinct ridge (Figs 6A, 24A, 27A). Medial to it the posterior part of the anterior vertical semicircular canal runs along the margin of the supraoccipital notch (Fig. 29A, B). This groove on the prootic apparently comes from the subarcuate fossa proper and could be the equivalent of the vascular duct described for *Oligokyphus* by Kühne (see p. 373).

The lateral ventral surfaces of the supraoccipital lie on the paroccipital parts of the opisthotics (Fig. 29C, SUOC, POP) and its lower medial surfaces lie on the exoccipitals (Figs 6A, 27, 28, 29C, SUOC, ORSCRFJ, OPO, EXO, POP). These contacts are simple sutura squamosa. On the occiput the lower end of the interparietal overlaps the medio-dorsal part of the supraoccipital and the medial part of each tabular overlaps the lateral dorsal parts of the supraoccipital (Figs 25A, 29C, IPAR, SUOC, TAB). On the occiput the tabular also encloses (Fig. 25A, TAB, PTF) the posttemporal foramen as described by Parrington (1946).

Opisthotic (Figs 1, 6, 24B, 25A, 27–29)

This bone forms the posterior part of the wall of the fenestra ovalis, and the prootic and basioccipital form the anterior part of the wall. The opisthotic separates the fenestra ovalis and jugular foramen of which it forms the anterior and lateral walls (Figs 25A, 27, FO, FJ, OPO). Posteriorly it meets the exoccipital (Figs 6, 25A, 27, 28, 29C, EXO) and postero-dorsally the supraoccipital (Figs 6, 25A, 27, 28, 29C, SUOC). The antero-dorsal part of the paroccipital process is formed by the prootic, and the remaining major part of the process is formed by the opisthotic (Figs 1, 25A, 29B, C, PRO, POP, OPO). The antero-dorsal face of the paroccipital process is excavated probably for the passage of veins (see Prootic above and Fig. 26) and the antero-ventral surface is also excavated to form the middle ear cavity which accommodates the stapes (Figs 1, 25A). The presence of a foramen of unknown significance featured by Estes (1961) and facing laterally in the paroccipital part of the opisthotic about midway between the posterior border of the fenestra ovalis and the antero-median border of the jugular foramen is confirmed (Figs 1, 25A, FN₂). Conceivably the internal jugular vein left the skull through this foramen and not with nerves IX, X and XI through the jugular foramen (foramen lacerum posterium).

Stapes (Figs 1, 19C, 25A, B, 26, 29A)

Both stapes are preserved and in both the stapedia foramen has a central position. Parrington's (1946) figure indicates that the stapedia foramen in his specimen lay more towards the distal end of the stapes. He suggested that in the young form the proximal surface of the head of the stapes was covered by cartilage about 1 mm thick. That the serially ground skull is not that of a fully grown animal is proved by the fact that much larger specimens have been described by other authors. Broom (1938*a*) has described a specimen of 88 mm, while Parrington's (1936*a*) specimen I was 85 mm. The present author has examined two skulls of more than 80 mm in length while the serially ground skull was only 67 mm. (All were measured from the tip of the snout to the end of the parietal crest with the possible exception of Broom's (1938*a*) specimen for which the maximum length may have been given.) It seems, therefore, that the central position of the stapedia foramen must be attributed to the youth of the specimen, and the consequent absence of an ossified cap on the head of the stapes. The proximal end of the right stapes does not quite reach the fenestra ovalis (Fig. 25A, FO), but if a cartilage cap were added it would fit into the cup surrounding the fenestra. A small process at the distal end of the stapes makes contact with the quadrate and this must represent a quadrate process in its correct position. Another even smaller distal process closely approaches the lower end of the groove in the squamosal which housed the external auditory meatus (Figs 1, 25A, B_{1,2,3}, QPS, ES). These processes are so delicate that their preservation can only be expected in an undisturbed stapes. It is therefore concluded that the right stapes is in the correct position and that its proximal end must have been capped by cartilage in life. Conceivably, however, some rotation

might have taken place soon after the death of the animal due to drying and consequent shortening of muscles and ligaments which held the stapes in position in the live animal.

The stapes on the left—although it appears to be in the natural position—has actually been pushed into the cup around the fenestra ovalis by the medial displacement of the quadrate and postdentary bones.

The anterior arm of the stapes (Figs 1, 25A, B_{2, 3}) is distinctly wider and stronger than the posterior arm. A small dorsal process (Figs 1, 25A, B_{1, 2, 3}, DPS), about 1 mm in length, curves upwards and slightly inwards from the posterior corner of the distal end of the stapes, towards the antero-distal end of the paroccipital process. A second process which the present author regards as the quadrate process of the stapes (Figs 1, 25A, B_{1, 2, 3}, QPS) extends ventrolaterally from the middle of the ventro-distal surface of the stapes to meet a similar, but slightly larger process, here called the stapedia process of the quadrate, which extends upwards from the postero-medial surface of the quadrate immediately above the medial part of the condyle (Figs 1, 19C, 25A, QPS, SPQ). A third very small process, here called the extrastapes (Fig 25A, B_{1, 2, 3}, ES), extends laterally from the distal surface of the stapes just in front of the dorsal process. It approaches the lower inner end of the groove in the squamosal for the external auditory meatus very closely. Ossification of the distal region of the stapes and especially of the processes seems to be incomplete, but there can be no doubt about their presence.

There is some difficulty in homologizing these processes with those described by Parrington (1946, 1949). The process here described as the quadrate process of the stapes may, if the stapes had rotated somewhat around its longitudinal axis, be Parrington's extrastapes. The dorsal process gives no difficulty, but the small process at its base, described here as an extrastapes, may conceivably be regarded as part of the dorsal process. The oblique flat face of the stapes at its antero-distal corner above the quadrate process may be regarded as the point of contact between the stapes and the quadrate.

Hopson's description of the *Thrinaxodon* middle ear is essentially correct, but it resembles the tritylodontid condition in structure, and probably function, more extensively than he implies. As in tritylodontids like *Bienotherium*, the stapes would be activated via the quadrate and articular in any jaw opening movement, but the function of this mechanism is unknown although it is a preadaptation to the mammalian condition.

Quadrate (Figs 1, 19B, C, 25A, 26, 29A, 31C, D)

Parrington (1946) described this bone very well and the present investigation largely served to corroborate his description. A foramen which he found in the quadrate '... median to the central thickening and a little way above the articulating surface' appears to be that of a small canal (Fig. 19C, QC) found in the displaced left quadrate. The canal runs transversely through the central thickening of the quadrate. In the intact quadrate this canal emerges on its lateral face

just behind the medio-dorsally directed process at the ventral edge of the quadratojugal. In its normal position (Fig. 26, Q) the quadrate lies in a pocket (Fig. 26, DQ) in the anterior face of the squamosal where it is held very loosely. The quadrate has a posteriorly directed flange which fits into a deep notch in the ventral border of the squamosal (Fig. 25A, QFL).

Olson (1944) and Parrington (1946) described a stapelial process of the quadrate (Figs 1, 25A, SPQ) which makes contact with a process of the stapes (see p. 379, Stapes). These authors have also shown that the posterior tips of the quadrate ramus of the pterygoid (QRPT) and the lateral lamina of the prootic (PROF) meet the medial surface of the quadrate (Figs 1, 19C, 26).

The quadrate is hollowed medially as in tritylodontids (Hopson 1966) and, as in these forms, is not buttressed firmly against the squamosal, although it still has no contact with the otic elements other than its medial contact with the lateral lamina of the prootic (see Figs 19C, 29A).

Quadratojugal (Figs 1, 19B, C, 25A, 26, 29A, B)

The present investigation has served to elucidate some features of this bone previously remarked on by Olson (1944) and Parrington (1946). The ventral end of the quadratojugal projects below the ventral border of the squamosal (Fig. 25A, SQ, QJ) but not sufficiently far down to make contact with the postdentary bones of the lower jaw normally. Contact may, however, have been established between the outer surfaces of the surangular and quadratojugal when the jaw was opened very widely (Fig. 25A, SAN). The upper part of the quadratojugal (Figs 1, 25A, QJFL) is expanded into a head, the dorsal surface of which is grooved (Fig. 26, GHQJ; Fig. 29B, QJ). The foot of the quadratojugal rests against the lateral surface of the quadrate at the base of the central thickening immediately above the lateral part of the condyle (Figs 25A, 26). The median surface of the vertical sheet of the quadratojugal (QJFL) and the lateral surface of the quadrate flange (QFL) are concave (Fig. 26). An anteriorly directed flange of the squamosal (Figs 1, 24C, 25A, 29A, SQS), which separates the quadrate and quadratojugal flanges, lies in this space between the concave surfaces of the two bones. A similar relationship is found in the cynognathids. The ventral surface of the foot of the quadratojugal is convex and fits into a concave quadrate surface (Figs 19B, 25A, 26, QJ, Q). The foot itself expands lateral to the vertical flange of the quadratojugal and the ventro-lateral part of the quadrate (Figs 1, 25A, 26). The lateral face of the quadratojugal flange is also concave, and another flange of the squamosal, expanded at its base, fits into the upper end of this concavity and helps to hold the quadratojugal in place (see e.g. Figs 1, 6B, 25A, 26).

Squamosal (Figs 1, 6B, 18A–20, 24C, 25A, 26, 29)

The present investigation added little to our knowledge of the squamosal. The pocket for the dorsal flange of the quadrate in the anterior face of the squamosal (Fig. 26, DQ) is only 1.6 mm deep. Another pocket (Fig. 26, DHQJ)

lies immediately lateral to the first and housed the grooved head of the quadratojugal (GHQJ). The anterior part of this pocket is confluent with that for the quadrate, but the posterior deeper part is initially separated from it by a thin wall of bone which expands posteriorly into the hind wall of the recess of the quadrate. The total depth of the pocket is 3,4 mm (Fig. 29B, QJ). Its posterior lower end is confluent with the deep notch for the quadratojugal flange in the posterior lower border of the squamosal. In anterior view the quadratojugal extends obliquely inwards and upwards into the pocket (see Fig. 26).

The tips of the quadrate ramus of the pterygoid (QRPT) and the lateral lamina of the prootic (PROF) reach the quadrate just in front of the inner wall of the pocket for the quadrate (Fig. 26). Crompton (1958: 191) has stated in error that in *Thrinaxodon* the quadrate ramus of the pterygoid does not reach the quadrate. In primitive cynodonts the quadrate rami of both the pterygoid and the epipterygoid reach the quadrate. The advanced cynognathids no longer retain the contact between the quadrate ramus of the pterygoid and the quadrate. *Cynognathus* does retain a contact between the epipterygoid and the quadrate. *Cynidiognathus*, which survived into Molteno Sandstone times (base of Stormberg Series overlying Beaufort Series), lacks this contact. Apparently the quadrate ramus of the pterygoid was withdrawn in early cynodonts and the quadrate ramus of the epipterygoid in late cynodonts.

Because the anterior surface of the paroccipital process is hollowed out, the antero-distal part appears as a distinct forward extension. This extension abuts against that part of the squamosal which forms the medial wall of the pocket for the quadrate (Figs 26, 29A, POPA). Because the distal surface of the paroccipital process does not make close contact with the squamosal (see e.g. Figs 26, 29B, POP, SQ), it seems reasonable to assume that the distal surface was covered by cartilage. Preservation of the distal end of the paroccipital process in *Cynidiognathus* (and possibly other cynognathids) also gives the impression that a cartilage cap may have been present. Such an arrangement might have been necessitated by some cranial kinetic movement at this point.

A distinct flange of the squamosal overhangs the posttemporal fossa (Fig. 2, PTF, SQ). This flange prevented constriction by the temporalis muscle of the veins (see above, Prootic, p. 373) which passed through the posttemporal fossa.

Orbitosphenoid

No trace of an orbitosphenoid was found in *Thrinaxodon*, but such an element was found in *Cynognathus* and *Cynidiognathus*, and has been described by Brink (1955a) in *Diademodon*.

Nasal septum and interorbital system

The presence during life of a nasal septum and an interorbital septum can be inferred from the structure of the vomer, the pterygoid and the parasphenoid. A groove runs along the median dorsal margins of the vomer and the para-

sphenoid (Fig. 6A, GR and all appropriate figures of sections). It seems probable that a nasal septum rested on the vertical plate of the vomer, a cribiform plate on the anterior part of the roof of the nasopharyngeal passage formed by the horizontal plate of the vomer, the palatine and the pterygoid, and an interorbital septum on the rostrum of the parasphenoid. No trace of an ossified interorbital septum similar to that found in *Cynognathus*, *Cynidiognathus*, and *Diademodon* was found. In these forms the median ossification is referred to as a presphenoid.

The existence of a cartilaginous posterior wall to the nasal capsule was suggested by Crompton (1958) for *Diarthrognathus* due to a difference in the matrix filling of the region where this structure would be expected. He suggested that such a difference in the matrix could be caused by finely suspended material which permeated through the more coarse material anterior and posterior to the space left by the disintegration of the cartilaginous wall. Possible evidence of a similar process was found in the sectioned skull of *Thrinaxodon*. The matrix in the nasal cavity itself is the same as that filling other cranial cavities and that surrounding the skull. In the left side of the snout a matrix which resembles fine quartz or calcite fills the space stretching from behind the posterior palatal foramina up to the choanae. This type of matrix differs conspicuously from the matrix found elsewhere in the skull.

Comparison with a model built of a sectioned skull of *Erinaceus europaeus* in the course of the present investigation shows that the position of this calcite-like matrix plate between the posterior palatal foramina and the choanae agrees exactly with the position occupied by a cribiform plate in a mammal. The problem is, however, that in mammals the secondary palate is more extensive posteriorly, so that the choanae are further back than in cynodonts. If the cribiform plate was indeed situated here in cynodonts there would apparently have been a gap between the posterior region of this plate and the interorbital septum further back. As this appears unlikely, the calcite-like filling should probably not be considered as an indication of a cribiform plate, or else its position is not a precise indication of the position occupied by the structure, the presence of which caused the calcite-like filling to develop. The presence of the calcite on the left side only may be a result of differences in the rate of disintegration of the possible cartilage.

Inner surface of the snout

A series of grooves and ridges on the inner surfaces of the nasals and frontals (Fig. 30A) is identical to those described by Watson (1913a) in *Nyctosaurus* and *Diademodon*. He considered these ridges and grooves, which closely resemble those in mammals, to be associated with the attachment of ethmoturbinals. On the inner surfaces of the maxillaries, similar but less pronounced ridges are found. These ridges may denote the presence of rudimentary maxilloturbinals. Similar grooves and ridges were also found in the cynognathids. Because this feature is generally associated with homiothermy it is interesting

to find it even in early cynodonts, where the possibility of incipient homiothermy therefore must be considered.

Internal ear (Figs 27–29C)

The description given by Olson (1944: 28–29) of the internal ear of *Thrinaxodon liorhinus* is confirmed by the present study. The sacculo-cochlear recess (Figs 27A–29B, COE, CO, SR) is fairly big and ovoid in shape. The fenestra ovalis is situated lateral to it. The recess lies on the same level as the floor of the braincase. The major part of the outer border of the fenestra ovalis is formed by the prootic, its posterior and part of its inner border by the opisthotic, and the anterior inner part of its border by the basioccipital, which also forms part of the medial border of the sacculo-cochlear recess. A thick bony wall of the opisthotic (Fig. 28, ORSUSR) demarcates the sacculo-cochlear recess from the utriculus. The separation of the sacculo-cochlear recess and the jugular foramen by a ridge of the opisthotic (Fig. 28, ORSCRFJ) is incomplete. The ampullar recesses (AAMP, HAMP, PAMP) and the courses of the semicircular canals (Figs 28, 29, AVC, HC, PVC) are described accurately by Olson (1944) and Estes (1961).

The channel identified by Estes as a fenestra rotunda, which joins the fenestra ovalis and the jugular foramen, is very distinct in the *Thrinaxodon* skull reconstructed from serial sections in the present investigation (Figs 25A, FNA, 27B). A reconstruction of the inner ear structures (Fig. 28) added little to the descriptions by Olson and Estes. (See also under Supraoccipital, p. 378.)

(b) LOWER JAW (Figs 2, 31–33)

New information obtained by serial grinding of a very well-preserved skull and lower jaw and reconstruction on an enlarged scale makes it necessary to reconsider some features described and discussed by previous authors. These new features pertain mainly to the angular, articular and dentary.

Angular (Figs 14, 15, 17A–19B, 20, 22B, 25A, 31C, D, 32)

The reflected lamina (ANRFL) of the angular is preserved on the left side (Figs 17C, 31C, D, 32B). Here it is crescent-shaped, but broad as figured by Olson (1944). On the right side it is broken off, but it is likely that a slender, curved piece of bone found in the matrix on the medial side of the right ramus is actually the lamina. Parrington (1946) described the structure as a broad sheet of bone. He suggests that the anterior and lower parts, being more substantial than the rest of the structure, tend to remain in specimens in which the delicate sheet has been lost by weathering or preparation. Comparison with other specimens in the National Museum, Bloemfontein, in which the reflected lamina is preserved, indicates that the loss of the thin sheet, as Parrington suggests usually happens, would give the structure a crescent shape.

Parrington's (1955) investigations led him to conclude that the masseter in

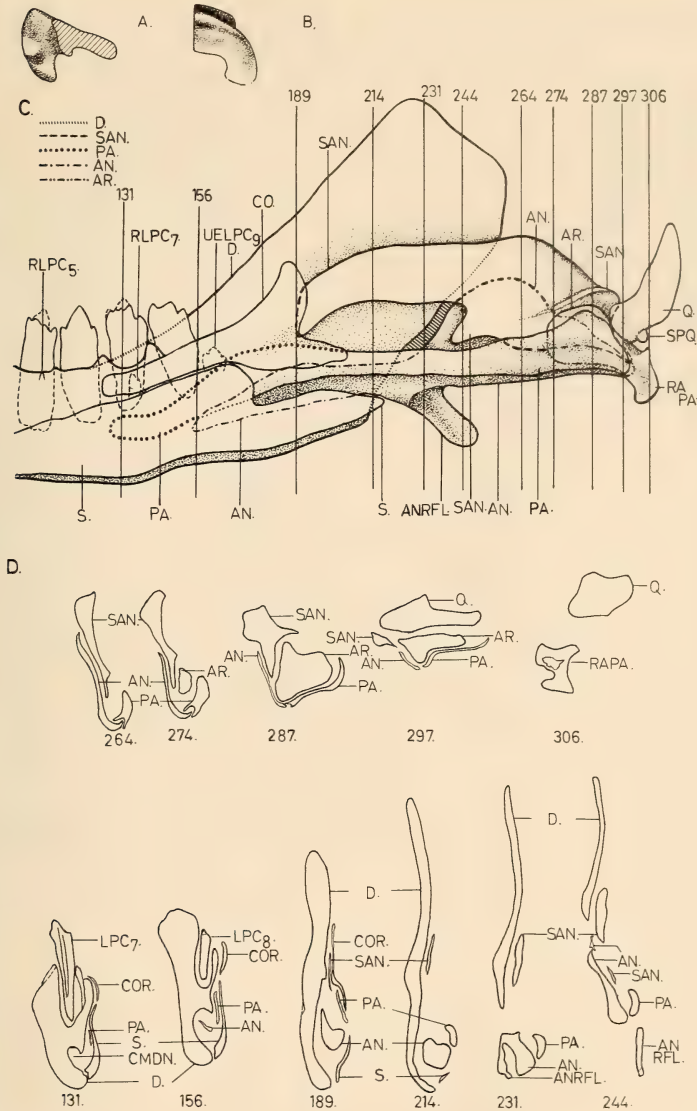


Fig. 31. A-B. Graphic reconstructions of anterior and medial views respectively of retroarticular process of articular on right side of serially sectioned skull. C. Graphic reconstruction of posterior part of lower jaw in medial view to show form, position and relationships of comprising elements. Important levels to show how dentary and postdentary bones are joined together are indicated by the numbers of the sections of the serially sectioned skull and lower jaw. D. Sections indicated in C. $\times 2$.

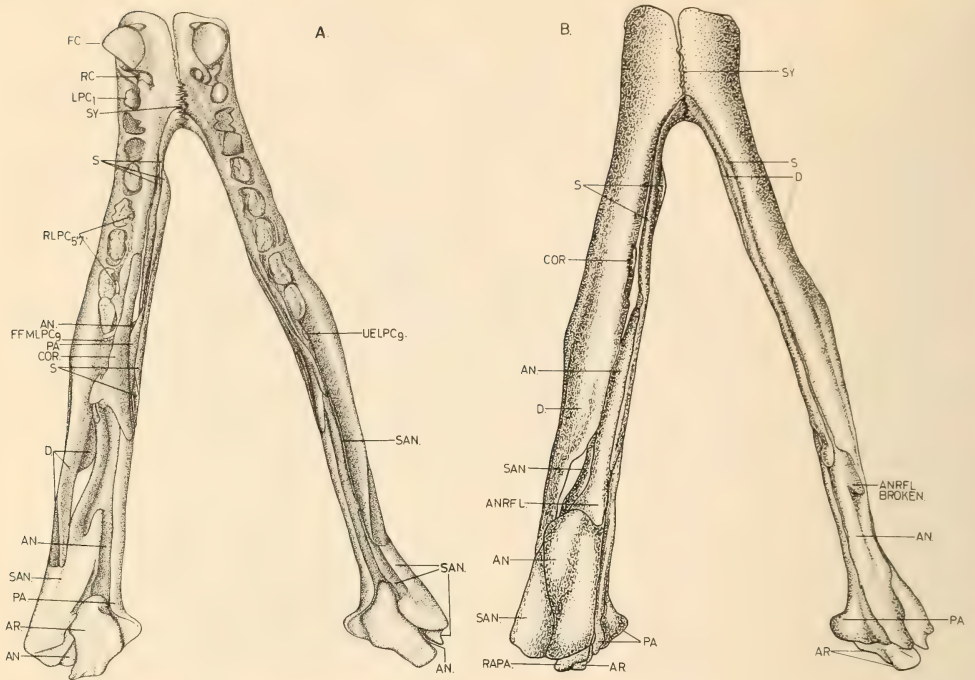


Fig. 32. Graphic reconstructions of lower jaw. A. Dorsal view; B. Ventral view. The latter is shown as a mirror image. $\times 1.5$.

gorgonopsids and in early cynodonts, like *Thrinaxodon*, was still inserted on to the reflected lamina of the angular. He suggested that the transfer of the insertion on to the dentary itself took place only in the advanced cynodonts with a large dentary. He believed that only then could the final reduction of the reflected lamina begin. Since the reflected lamina in *Thrinaxodon* is, however, already very much smaller than in *Gorgonopsia* and *Therocephalia*, and even slightly smaller than in procynosuchids, it appears probable that at least a large part of the masseter muscle must already have shifted its insertion on to the angle of the dentary. The very small reflected lamina figured by Broili & Schröder (1934a, 1935a) for *Cynognathus*, and the equally small one in *Trirachodon* specimens in the National Museum and in *Diademodon*, give the impression of it being a disappearing structure. It seems, therefore, that the reflected lamina had served

initially as insertion for the masseter muscle as Parrington (1955) concluded, but that it was already becoming unnecessary in the Middle Beaufort cynodonts where the masseter was already largely if not completely inserted on to the angle of the dentary.

Crompton (1963*b*) in his discussion of the origin of the mammalian lower jaw and its musculature accepted Parrington's suggestion that the masseter transferred from the reflected lamina on to the angle of the dentary. He suggested that there had been a superficial masseter inserting on the reflected lamina, and a deep masseter inserting on the postdentary bones. Migration of these muscles on to the dentary would have caused the reduction of the elements on to which they inserted.

Barghusen (1968) rejects these interpretations. On the basis of modern reptiles he believes that three muscles may originally have attached to the angular keel and massive reflected lamina in sphenacodonts and early therapsids. Of these three muscles he considers the branchiomandibularis as the most likely to have retained its attachment to the reflected lamina in cynodonts after the possible earlier pterygoideus musculature had been lost and the intermandibularis had shifted entirely on to the enlarged dentary, causing the reduction of the reflected lamina. He also concluded that the cynodonts indeed developed a masseter-like muscle, but in a manner different from that proposed by Parrington or Crompton. He believes that it differentiated from the external adductor and achieved insertion on the lateral surface of the dentary in primitive cynodonts. This insertion then migrated downwards to the postero-ventral edge of the dentary in later cynodonts. This development is uniquely cynodont and closely approaches the adductor jaw musculature of mammals. This is one of the reasons why cynodonts appear better fitted than any other group as the ancestors for all mammals.

Articular (Figs 19, 20, 31, 32)

The articular (AR) is held closely between the posterior lower half of the surangular (SAN) and the posterior part of the prearticular (PA) medially (Figs 31C, D_{274, 287, 297}, 32). It is a short solid bone with a pronounced bulge (Fig. 32A) towards the prearticular. Its median-dorsal surface is concave (Fig. 31D₂₈₇), a feature which is more pronounced along the central part of the bone than along its posterior part.

This concave median-dorsal surface results in a latero-dorsal ridge (Fig. 31B, D₂₈₇), which is made more pronounced because the vertical diameter of the bone is larger along the lateral margin of the bone than along the medial bulge. This bulge becomes progressively less distinct towards the posterior end of the bone, where it ends as a ridge on the upper medial surface of the retro-articular process (RAPA) (Fig. 31B, D_{297, 306}). Another ridge only becomes perceptible behind the central part of the bone. It runs backwards from the ventro-lateral surface (where it originates as a result of the medially directed bulge) to a ventro-median position, becoming progressively more distinct on

its way. Finally it terminates in the retroarticular process which is deflected downwards and forwards (Figs 31A, D_{287, 297, 306, 32B}).

The presence of a well-developed retroarticular process in *Thrinaxodon* has apparently not been described previously. Such a process is preserved only on the right articular of the serially ground skull (Figs 31A, B, C, D_{306, 32B}, RAPA) and is missing in all the other *Thrinaxodon* skulls in the National Museum. Apparently the retroarticular process in *Thrinaxodon* is particularly apt to break off either prior to fossilization or later during exposure and weathering.

Parrington (1955) discusses the mechanics of retroarticular processes. He examines the deflected articular process found in synapsids generally, and concludes that this deflected process is a true retroarticular process which gave attachment to a depressor mandibuli muscle in all the synapsids. This conclusion contradicts that of Watson (1948, 1951) who believes that in late synapsids the true retroarticular process had for the most part disappeared, and with it the depressor mandibuli muscle. According to Watson the posterior pterygoid muscle attached to the structure, which Parrington calls a retroarticular process in the late synapsids, and sublingual muscles (or muscles comparable with those of mammals) opened the jaw. Parrington shows that the functional implications of this determination raises grounds for doubting Watson's interpretations. An interpretation of the disputed structure and its modifications as a retroarticular process allows for a straightforward explanation in terms of jaw-mechanics.

Dentary and splenial (Figs 2-4, 8, 9, 11, 14, 15, 17A-18B, 22B, 31C, D, 32)

Each lower jaw ramus is formed mainly by the dentary which is joined by an interdigitated suture only at its extreme anterior end to the dentary of the opposite ramus (Fig. 32, SY). The posterior part of the lower jaw symphysis is formed by an interdigitated suture between the two opposite splenials (Fig. 32, S). The anterior part of the splenial which takes part in the symphysis, is thick and solid (Fig. 8A, S) compared with the rest of the bone which has a thin upper and somewhat thicker lower part (Figs 9, 11, 14, S). The splenial lies against the lower half of the medial surface of the dentary where the expanded lower end of the splenial fits into an excavation along the lower part of the dentary.

Due to the loss of the incisor bearing part of the mandible, the mandibular canal (Figs 8-10, CMDN) for the ramus mandibularis of the trigeminal nerve could not be traced further forward than the canine alveolus into the base of which it enters. The major part of the canal anterior to the seventh postcanine lies entirely in the dentary. It runs just below the bases of the postcanine alveoli, with each of which it retains contact. Behind the seventh alveolus the medial wall of the canal is formed by the splenial. The anterior end of the prearticular, which is inserted between the medial surface of the dentary and the upper part of the splenial, extends forward to this level where the mandibular canal enters the dentary (Figs 11B, 31C, D_{131, 32, PA}). The tip of the prearticular lies just above

the mandibular canal. This bone, which is very thin, is expanded dorso-ventrally for some distance behind the level of the eighth lower postcanine (Fig. 31C, PA). Its lower end reaches down below the upper medial dentary margin of the mandibular canal. Thus it forms the upper part of the medial wall of the posterior part of this canal into which the anterior end of the angular penetrates as far as the eighth postcanine (Fig. 31C, D₁₅₆, AN). Above the mandibular canal behind the seventh postcanine, the medial surface of the dentary is slightly concave, apparently to aid in the attachment to the dentary of the prearticular and splenial, and further back the coronoid (Figs 14–15B, D, S, PA, COR). The channel in the dentary behind the seventh postcanine becomes progressively higher. The medial part of its upper wall is formed by the lower surface of the tooth-bearing ridge (Figs 11B, 14A, B). Where this structure ends well behind the anterior border of the coronoid process of the dentary, a medio-ventrally directed ledge forms the upper wall of the channel for approximately a further 5 mm. Behind this ledge there is no further indication of the mandibular canal.

The anterior end of the angular which penetrates into the mandibular canal divides it into an upper and a lower half. Along the dorsal surface of the angular runs a groove of which the lateral wall is considerably higher than the medial one. This groove extends as far back as the angle of the dentary (Figs 14, 15, D, AN). Still further back the reflected lamina (ANRFL) is attached to the base (Fig. 17B, C) of the angular and immediately behind this level the angular is considerably expanded in a dorsal direction (Figs 31C, D₂₄₄, AN). This part of the bone is tilted laterally, with its dorsal margin directly below the lower margin of the coronoid process of the dentary. This part of the angular has a peculiarly contoured shape to maintain a close relationship between itself, the prearticular and the surangular. This latter bone lies against the inner surface of the upper half of the angular which is curved in such a way as to form a ledge for the support of the surangular, the posterior half of which is expanded in a ventral direction (Figs 31C, D_{264, 274}, 32A, AN, SAN). The lower margin of the posterior half of the angular is curved medio-dorsally and fits into a groove along the ventral surface of the posterior part of the prearticular (Figs 31D_{264, 274, 287}, 32B, PA) thus forming a schindylesis or wedge-and-groove suture. Anterior to the reflected lamina of the angular, the prearticular lies at the medio-dorsal margin of the angular. Because the lateral surface of the prearticular is concave, a channel is formed between the concave dorsal surface of the angular and the concave lateral surface of the prearticular (Figs 31D_{156–274}, 32A, AN, PA).

The articular inserts into the posterior part of this channel (Figs 31D_{274, 287, 297}, 32A, AR). Its anterior dorsal surface is concave (grooved) and covered laterally by a peculiar ledge of the surangular (Figs 31C, D_{274, 287}, 32A, SAN).

A possible course for the ramus mandibularis of the trigeminal can now be suggested. It probably ran backwards in the mandibular canal; then along the dorsal surface of the angular where the latter penetrates into the canal; then along the channel formed by the dorsal and further back the medio-dorsal

surface of the angular and the lateral surface of the prearticular; then along the dorsal surface of the anterior part of the articular which inserts into the angular-prearticular channel. From the articular, but in front of the quadrate, the ramus mandibularis probably passed sharply medianly and dorsally in front of the stapes. At its base the lateral lamina of the prootic is notched on its anterior margin. Passing through this notch the ramus mandibularis then probably entered into the cranial cavity via the large foramen between the prootic and epipterygoid.

Coronoid (Figs 11B, 14A–15B, 31C, D, 32A)

The tip of the coronoid lies just behind the sixth postcanine. The bone extends along the medio-dorsal surface of the dentary above the splenial, prearticular and angular. In this region the upper part of the coronoid lies above the dorsal margin of that part of the dentary which forms the medial wall of the eighth postcanine alveolus. The ninth postcanine alveolus, which is partly formed, has a crown of an unerupted tooth of much smaller size than the eighth in it. The dentary has hardly any part in the formation of the medial wall of the ninth alveolus. The coronoid covers the partly formed ninth alveolus medially (Figs 14B, 31C, 32A, COR, UELPC₉). Behind this ninth alveolus the coronoid increases considerably in height (Figs 31C, 32A, COR). Its upper part is thicker than its lower edge which covers the upper edge of the prearticular (Figs 15A, B, 31C, COR, PA). The medial surface of the coronoid process of the dentary behind and above the postcanine alveoli is concave to receive the upper part of the coronoid (Figs 15A, B, 31D₁₈₉, D, COR). Just behind the tip of the surangular which is inserted between the coronoid and the dentary, the coronoid bifurcates into an upper part which ends abruptly and a lower part which extends backwards for about 3,5 mm along the upper part of the medial surface of the prearticular (Figs 31C, 32A, COR, PA).

Surangular (Figs 17A–19B, 20, 22B, 25A, 31C, D, 32)

The surangular has a long anterior portion. This part of the bone is very thin and lies in a shallow depression on the medial surface of the coronoid process of the dentary. On the lateral surface of this coronoid process is a ridge, the position of which (Fig. 31D_{214, 231, 244}, D, SAN) corresponds with the medial depression for the surangular. This ridge, which runs obliquely upwards towards the posterior margin of the dentary, forms the lower margin of the insertion area of the masseter muscle.

Towards and beyond the posterior margin of the coronoid process of the dentary the long anterior and the posterior parts of the surangular become progressively thicker. Well behind the coronoid process and above the reflected lamina of the angular, the surangular bears an antero-ventrally directed process, 2 mm long, below the long anterior part of the bone. The base of this process is that part of the bone which is expanded in a ventral direction and lies medial to that part of the angular which is expanded in a dorsal direction (Figs 31C,

32A, SAN, AN). The relationships of the angular and surangular have been described above (see p. 389).

Some reference has been made to the relationship between the surangular and the articular (see p. 387). The lower edge of the surangular lies against the lateral surface of the articular. Less than 2 mm anterior to, but above the tip of the articular, a ridge begins on the medial surface of the surangular (Figs 31C, 32A, AR, SAN). Further back this ridge progressively expands into a ledge running above the lateral part of the articular. The upper half of the surangular, which has a concave medial face and a thickened dorsal edge, ends on the ledge (Figs 31C, D_{264, 274, 287}, 32A, SAN). The ledge itself ends just behind the bulky anterior part of the articular, and the thin lower edge of the bone ends along the flattened neck about half-way between the anterior part of the articular and the retroarticular process (Figs 31C, D₂₉₇, 32A, AR, SAN, RAPA).

Prearticular (Figs 11B, 14A–15C, 17A–19B, 20, 22B, 25A, 31C, D, 32)

The relationships of the prearticular with the dentary and splenial (see p. 388) and with the angular (see p. 389) have been described above. It can also be noted that the posterior part of the prearticular, of which the ventral margin is grooved for insertion of the medio-dorsally curved ventral margin of the angular, is increasingly tilted medially further back where it is a broad thin plate. This structure is correlated with the rapid progressive increase in diameter of the anterior part of the articular of which the medial surface is covered by the prearticular which closely follows its contours (Figs 31D_{287, 297}, 32A, AR, PA). Only between the postero-dorsal part of the medial face of the articular, and the postero-dorsal part of the lateral face of the prearticular is there an interspace which may be an indication of the presence of the tensor tympani muscle (Fig. 31D₂₉₇). In mammals this muscle is typically inserted on to the medial surface of the malleus, which is considered homologous with the articular and runs forward to its origin on the base of the skull.

(c) DENTITION (Figs 1, 3–11B, 13B₂–14B, 31C, D, 32A, 33)

A detailed description of the dentition of *Thrinaxodon liorhinus* is deemed unnecessary because of the work done by Crompton and co-workers in recent years. However, since they limited their studies to the postcanines, a few points of interest about the incisors and canines revealed by the study on which this paper is based may be mentioned.

Specimens actually investigated by the present author or described in the literature reveal evidence of at least four replacements of the incisors between the 35 mm and the 88 mm skull-length stages. Crompton (1955c) has pointed out that in the cynodonts investigated by him replacement of incisors and canines is found much more frequently than replacement of postcanines. This phenomenon is due, he believes, to the fact that incisors and canines form an arc whereas postcanines form a linear series. During growth those parts of the

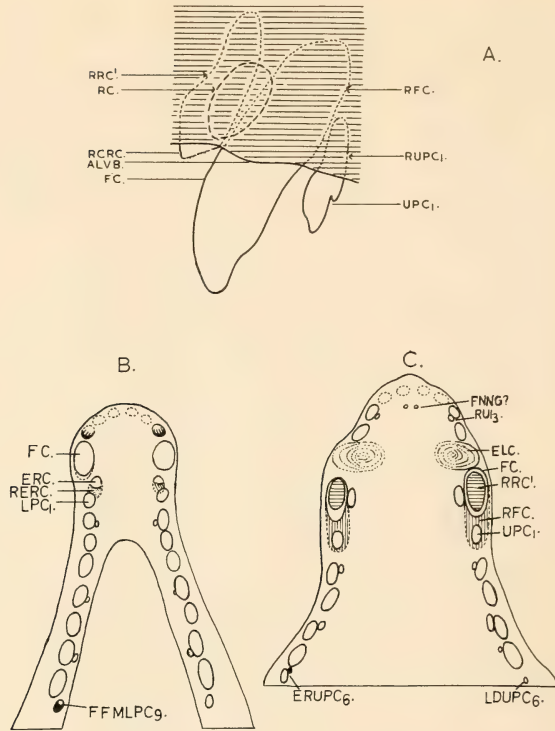


Fig. 33. A. Graphic reconstruction to show relative positions of replaced, functional and replacing upper canines. B-C. Graphic reconstructions of lower and upper dentitions. Only outlines of teeth crowns are shown and replacing postcanines are shown in their true position with respect to the functional teeth. Lost incisors are indicated by dotted outlines only. Alveoli of lost replacing teeth are shown in black. A $\times 2,5$. B-C $\times 1,25$.

mandible and upper jaw containing incisors and canines increase greatly in size. Frequent replacement of the functional teeth by larger ones would, therefore, ensure that functional teeth occupied the entire region.

The current investigation of *Thrinaxodon* and the later cynodonts shows that the type of replacement of the canines in these forms is identical with that found by Kermack (1956) in the therocephalians and gorgonopsians which he investigated. Although the crowns of the canines are apparently shed, the roots are retained (Figs 3, 33A, (R)RC¹) and are gradually resorbed, thus apparently aiding the calcium (and phosphate?) metabolism of the animal. There is some evidence that the alternation of consecutive generations of functional canines between the anterior and posterior halves of the alveolus, observed by Kermack, can also take place in *Thrinaxodon*. One example of an upper replacing canine

erupting posterolingual to the functional one was found. In all other specimens investigated the replacing canine was anterolingual to the functional one. Evidence of the bone plug which closes the unoccupied part of the alveolus until the new canine erupts, was found in the lower canine alveoli of the sectioned skull (Fig. 3A, BP). Consideration of all available evidence suggests at least six and probably seven or more replacements of the functional canines.

SUMMARY

1. A skull of *Thrinaxodon liorhinus* has been serially sectioned at intervals of 200μ , and an enlarged wax model built. New details on the structure of the component bones of the skull and their relationships are described and figured. The processes of the premaxillary and their contacts with the maxillary are described and figured. The canals in the maxillary are described and functional and replacement teeth are indicated. The canals in the lacrimal and the relationships of this bone with the maxillary and palatine to form the maxillary antrum are indicated. Grooves and ridges on the inner surface of the roof of the snout, possibly for the attachment of turbinals, are figured.

The vomer with a groove along its dorsal margin is described and it is shown that the double anterior end suggests a paired origin of the bone. The relationships of the premaxillary with the lower end of the vomer are indicated as well as a possible explanation for the thickened lower margin of the anterior vertical part of the bone and the medial dorsal margins of the maxillaries. An explanation is also offered for the ridges on the ventral surface of the palatine and pterygoid. The exact relationship of the posterior parts of the pterygoids and the parasphenoid rostrum is indicated. It is shown that interdigitated sutures preclude the possibility of kinetic movement in this region. It is suggested that the groove dorsally along the vomer, and on the dorsal surface of the parasphenoid rostrum, may indicate the presence of a cartilaginous nasal septum and an interorbital septum. Evidence in the matrix of a possible cartilaginous cribriform plate at the posterior end of the snout is described. The relationship of the anterior ventral part of the epipterygoid and the pterygoid is indicated as well as that of the epipterygoid and prootic. The walls of the braincase are described in detail, externally and internally. The interpretations of Watson and Cox of the venous system on the walls of the braincase in cynodonts and anomodonts are compared with conditions in *Thrinaxodon* and an interpretation of the condition in this form is suggested.

The structures of the prootic and opisthotic to accommodate the internal ear structures are described and figured. The presence of a possible fenestra rotunda is confirmed. The exact way in which the abducent foramen is formed is described. The possible courses of the maxillary, mandibular and deep ophthalmic rami of the trigeminal, the abducent and the palatine ramus of the facial nerves are described. A possible Eustachian foramen is indicated as well as a possible separate foramen for the internal jugular vein. The basicranial region is described and it is shown that the sella turcica is very shallow and that there

is hardly any dorsum sellae. The stapes is described in detail and it is shown that it has three processes on its distal end; these are a dorsal process towards the paroccipital, a quadrate process, and, as preserved, a minute process towards the base of the external auditory meatus. The relationships of the quadrate and quadratojugal with each other as described by Parrington (1946) are confirmed and their relationships with the squamosal are described. Parrington's (1946) description of a canal penetrating the quadrate is confirmed. A stapelial process on the quadrate is described. The elements of the lower jaw are described in detail and their relationships with each other are figured in different views. A retroarticular process is described for the articular.

2. It is shown that the incisors are replaced at least four times and that during replacement the crown of the functional canine is shed, but that the root is gradually resorbed. Only one example of an upper replacing canine erupting postero-lingual to the functional one was found. In all other specimens investigated the erupting replacing canine was in the antero-lingual position in relation to the functional canine. More definite evidence of the alternation of the functional canine between the anterior and posterior halves of the alveolus seems to be needed.

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KEY TO LETTERING

AAMP	anterior ampulla
ADP	antero-dorsal process of the prootic
AN	angular
ANRFL	reflected lamina of the angular
AR	articular
ARCA	attachment of the rectus capitis anticus muscle
AVC	anterior vertical semicircular canal
AWELC	premaxillary part of the anterior wall of the excavation for the lower canine
BCP	basicranial process
BO	basioccipital
BP	bone plug
BPTP	basipterygoid process of the basisphenoid
BPTPL	basal plate of the epipterygoid resting on the basipterygoid process
BQREPT	broken quadrate ramus of the epipterygoid
BSCROPPT	continuation on to the basisphenoid of the ridge formed by the outer prong of the pterygoid.
BS	basisphenoid
BSY	broken symphysis
CC	crus communis
CCA	carotid canal
CEPT	cavum epitericum
CH	choanae
CMDN	canal for the mandibular nerve
CMN	canal for the maxillary nerve
CO	cochlea
COE	cochlear extension
COR	coronoid
CPD	damaged coronoid process of the dentary
CPR ^{vii}	canal for the palatine ramus of the facial nerve
CRMAX _v	probable course of the maxillary ramus of the trigeminal nerve
CROP _v	probable course of the ramus ophthalmicus profundus of the trigeminal nerve
CRPAL ^{vii}	probable course of the palatine ramus of the facial nerve
CV	vena communicans between vena capitis dorsalis and vena capitis lateralis
D	dentary
DF	displaced fragment
DFPT	displaced fragment of the transverse flange of the pterygoid
DG	depression for a gland
DHQJ	depression on the squamosal for the head of the quadratojugal
DLBMN	duct for the lacrimal branch of the maxillary nerve
DORS	dorsal
DPS	dorsal process of the stapes
DQ	depression for the quadrate on the squamosal
DRUPC ₂	displaced second replacing upper postcanine
DT	displaced tooth
DTCMN	double termination of the canal for the maxillary branch of the trigeminal nerve
DV	double anterior end of the vomer
EAM	external auditory meatus
EDLBMN	entrance of the duct for the lacrimal branch of the maxillary ramus of the trigeminal nerve
EIMC	entrance of the independent maxillary canal
ELC	excavation for the canine of the lower jaw
ELD	entrance into lacrimal duct
EPT	epipterygoid
EPTR	ectopterygoid
ERC	erupting replacing canine
ERUPC ₂	erupting replacing second upper postcanine
ES	extrastapes

EUPC	erupting upper postcanine
EXO	exoccipital
FC	functional canine
FDTCMN	foramina of double termination of canal for the maxillary ramus of the trigeminal nerve
FEPTR	foramen in the ectopterygoid
F _v	foramen for trigeminal nerve
F _{vi}	foramen for abducent nerve
F _{vii}	foramen for facial nerve
F _{xii}	foramen for hypoglossal nerve
F	frontal
FFMLPC ₉	displaced main fragment of the developing ninth lower postcanine
FIMC	foramen of the independent maxillary canal
FIN	foramen incisivum
FJ	foramen jugulare
FLA	foramen lacerum anterium
FLBMN	foramen for the lacrimal branch of the maxillary ramus of the trigeminal nerve
FM	foramen magnum
FN ₁	foramen for Eustachian tube (?)
FN ₂	foramen for internal jugular vein (?)
FNA	fenestra rotunda
FNNG	foramen of canal to Organ of Jacobson and nasal gland
FO	fenestra ovalis
FPOP	fragment of the paroccipital process
FPT	foramen pterygoideum
FRAC	fracture
FSA	fossa subarcuata
FSC	foramen for the vena capitis dorsalis in the sinus canal
GDV	groove along the dorsal margin of the vertical plate of the vomer
GHQJ	grooved head of the quadratojugal
GR	groove
GRPR _{vii}	groove for the palatine ramus of the facial nerve
GRVSC	groove for the vein of the sinus canal
HAMP	ampulla for the horizontal semicircular canal
ICF	internal carotid foramen.
IDIOPPT	excavation on pterygoid beyond which the inner and outer prongs separate
IMC	independent maxillary canal
INPPX	internarial process of the premaxillary
IPAR	interparietal
IPPT	inner prong of the pterygoid
J	jugal
KVP	keeled vomer plate
KVPG	keeled vomer plate with groove
L	lacrimal
LD	lacrimal duct
LDUPC	remnant of the lost developing sixth upper postcanine
LEX	lingual excavation
LF	lacrimal foramen
LLCL	recess for the lateral lobe of the cerebellum
LLF _{xii}	large lower foramen of the hypoglossal nerve
LPC _x	lower postcanine number x
LRC	replacing lower canine
MAN	maxillary antrum
MP	mastoid process
MPPX	maxillary process of the premaxillary
MX	maxillary
MXPS	maxillary-palatine suture
N	nasal
NO	nostril

O	orbit
OPO	opisthotic
OPPT	outer prong of the pterygoid
ORSCRFJ	opisthotic ridge separating the cochlear recess and the jugular foramen
ORSUSR	opisthotic ridge separating utricular and saccular recesses
P	palatine
PA	prearticular
PAMP	posterior ampulla
PAO	pila antotica
PAR	parietal
PCP	cultriform process (= rostrum) of the parasphenoid
PF	parietal foramen
PITF	pituitary fossa
PO	postorbital
PODG	postdentary groove
POP	paroccipital process
POPA	paroccipital process abutting against the squamosal
POPARS	postorbital-parietal suture
PPF	posterior palatal foramen
PPLMX	palatal plate of the maxillary
PPPX	palatal process of the premaxillary
PPPXSP	short prong of the palatal process of the premaxillary
PPRASP	posterior palatine part of the ridge for the attachment of the soft palate
PRF	prefrontal
PRO	prootic
PROF	prootic flange
PRON	inner fork of the antero-dorsal process of the prootic
PS	parasphenoid
PS-BS	parasphenoid-basisphenoid
PT	pterygoid
PTF	posttemporal fossa
PTPOF	pterygo-paroccipital foramen
PTPRQ	pterygoid process of the quadrate
PTPSS	pterygoid-parasphenoid suture
PTRASP	pterygoid part of the ridge for the attachment of the soft palate
PVC	posterior vertical semicircular canal
PVCJUT	posterior vertical semicircular canal joins utriculus
PX	premaxillary
Q	quadrate
QC	quadrate canal
QFL	quadrate flange
QJ	quadratojugal
QJFL	quadratojugal flange
QJN	notch for the flange of the quadratojugal
QN	notch for the flange of the quadrate
QPS	quadrate process of the stapes
QREPT	quadrate ramus of the epipterygoid
QRPT	quadrate ramus of the pterygoid
RAMCP	ridge for the attachment of the mucous covering of the palate
RAPA	retroarticular process of the articular
RASP	ridge for the attachment of the soft palate
RC	replacing canine
RC ¹	root of the replaced canine
RCRC	remains of the crown of the replaced canine
RERC	root of the erupting replacing canine
RFC	root of the functional canine
RFMLPC ₉	remaining fragment of the 9th lower postcanine
RHC	rhinial canal
RLPC _x	X-th replacing lower postcanine

ROLI ₃	root of the third lower incisor
ROVCL	root of the vena capitis lateralis
RRC [†]	root of the replaced canine
RUI ₃	replacing third upper incisor
RUPC _x	X-th replacing upper postcanine
SAC	sacculus
SAN	surangular
SC	sinus canal
SET	sella turcica
SF	stapedial foramen
SMX	septomaxillary
SPBPPPX	small process at the base of the palatal process of the premaxillary
SPQ	stapedial process of the quadrate
SPRO	spur of the prootic
SQ	squamosal
SQS	flange of the squamosal protruding forward between the quadrate and quadrato-jugal
SR	saccular recess
S	splenic
ST	stapes
STR	stapedial recess
SUOC	supraoccipital
SY	symphysis
TAB	tabular
TCP	thin coronoid process
TFPT	transverse flange of the pterygoid
UELPC ₉	ninth lower postcanine which had not yet erupted
UI ₃	third upper incisor
UPC _x	X-th upper postcanine
UPPPPX	upper prong of the palatal process of the premaxillary
UR	utricular recess
USW	unossified side wall of the braincase
UT	utriculus
UZ	unossified zone
V	vomer
VCD	vena capitis dorsalis
VCL	vena capitis lateralis
VG	venous groove
VP	vomer plate
VPAR	vena parietalis
WPS	wing of the parasphenoid
WQRSQ	wall of the recess for the quadrate on the squamosal
WST	wall of the sella turcica